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THE UNIVERSITY OF ALBERTA

PRIMARY PRODUCTION PROCESSES WITHIN POLAR SEMI-DESERT VEGETATION, TRUELOVE LOWLAND, DEVON ISLAND, N.W.T., CANADA

by

© Josef Svoboda

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

IN

PLANT ECOLOGY.

DEPARTMENT OF BOTANY

EDMONTON, ALBERTA

FALL, 1974.

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "PRIMARY PRODUCTION PROCESSES WITHIN POLAR SEMI-DESERT VEGETATION, TRUELOVE LOWLAND, DEVON ISLAND, N.W.T., CANADA" submitted by Josef Svoboda in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Plant Ecology.

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ABSTRACT

Plant communities, their production and some production processes were studied on raised beaches in the High Arctic, Devon Island for three years. Historical prospectives of the site and area are outlined. On crests and slopes of these beaches a cushion plant-lichen community is present while the "foot" of the beach which forms a transition to the adjacent meadow is occupied by a cushion plant-moss community. Soil, microclimate, vascular plant phenology, growth and distribution of vascular plants across the raised beach were also studied. Vascular plant cover is low, ca. 20% on crests and 60% in transitions, and so are aboveground and belowground standing crop (350 - 400 $g.m^{-2}$) and seasonal production (ca. 22 $g.m^{-2}$). Chemical analyses of soil and plants showed a low content of some minerals (N, P, K) but a high content of Ca.Carbohydrate levels were very low (ca. 1 to 3%) in cushion plants but relatively high in soft herbs (ca. 30%). Also, chlorophyll, lipids and other compounds were analysed. *Dryas integrifolia* was chosen for more detailed aut-ecological study and served as representative species of the community in respect to form and function. Raised beach ridges were recognized as a Polar Semi-desert habitat, autonomous and genuine in microclimate as well as vegetation.

PREFACE AND ACKNOWLEDGMENT

The Polar Region - a unique part of the Earth, with extremities and anomalies making life difficult for animals and even plants. Hard to man but after all, kind and friendly. Barren lands exposing silently the rocky surface to the elements where the ice has still valid lease to occupy thousands of square kilometers, where lichens with not many other "higher" plants, invertebrates and birds are the first messengers of life.

The author of this thesis came to Canada from a small European country which has no arctic regions, but nevertheless an arctic social climate. He would not have believed that he ever would see regions first described and introduced to his mind by an almost unknown pioneer in the Arctic, the Czech-Canadian Jan Welzl who spent "in the Golden North", 50 years of his long and unbelievably adventurous life. To this simple, brave man, whose body rests in the cold ground of Dawson City, this work is dedicated.

The author was granted the favor to work for three years with the IBP High Arctic Project team of experienced scientists and young scientific recruits not less unexperienced in the Arctic than he was but devoted and inquisitive. Some of these men, colleagues and soon friends deserve to be mentioned because of their direct or indirect influence on this work. These are: Dr. L.C. Bliss, director of the Canadian IBP Tundra Biome Project in Truelove Lowland and the author's patient and inspirative advisor, Dr. J.M. Mayo, tacit enthusiast under midnight sun, Dr. G.H. La Roi with a taste for creative fantasy in science, Dr. D.W.A. Whitfield, systems analyst with human understanding for the complexity of things and the simplicity of minds, and colleague

Jim Ryan, salt and pepper of the arctic human stew.

Paralleling this work dealing with plant production of Polar Semi-desert habitats, the author's colleague Michael Muc, conducted an intensive production study on the lowlands meadows. These two theses represent one coordinated work in two volumes so to speak where some aspects and topics overlap and others complement. Many problems, theoretical and practical, were discussed together. Three years of cooperative field work as well as dwelling under the common roof of the Bioscience Building of the University of Alberta marked both papers with the characters of twins. Twins nevertheless self-sustaining, in a friendly sense jealously independent and anxiously demanding their own identity.

The author is indebted for the field assistance of Mr. Ken Orich (1970), Miss Dawn Dickinson and Mr. Doug Peters (1971) and to Miss Lewina Laung (1972). He admits that he took advantage of the fact that in the High Arctic time can be divided into days only with difficulties. As a result the quantity of collected data was enormous every summer. Even more the author expresses thanks for the laboratory work, especially for the precise calorimetric and carbohydrate analyses to his wife Kveta. Further sincere acknowledgments belong to Miss Kathy Smith and Miss Donna Kittle for their devoted help with completion of laboratory analyses. Special credit is granted to the project analyst Dr. Doug Whitfield and two of his assistants Miss Vivian Mahoney and Mr. Ross Goodwin for banking and computer processing most of the data collected.

This project was supported by NRC A4879 and NRC-CCIBP grants to Dr. L.C. Bliss. Logistic support was courteously offered by

Imperial Oil, King Resources, Polar Continental Shelf Project (PCSP) and Sun Oil. Arctic Institute of North America granted accomodation in its Truelove Lowland Base camp.

Realizing for long that our never ending search for the exciting truth is mere a tracing the work of the first and only real Author, the utmost thanks for completion of this imperfect outline belong to God.

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"All men by nature have a desire to know."

Aristotle
On Man in the Universe.

INTRODUCTION

In the High Arctic, those lands north of 70th parallel, terrestrial life is a "marginal phenomenon", reaching its maximum in coastal lowlands and narrow valleys. At these latitudes the Ice Age left 5,000 to 9,000 years ago and the land surface still retains all characteristics of a periglacial environment: rigorous climate, deep permanently frozen and patterned ground, large masses of ground ice, etc.

The high arctic coastal lowlands are analogous to desert oases. Their vegetation is more lush and animal life is mostly concentrated there, compared to that of the surrounding vast uplands. The lowlands are limited in size and form discrete units in which trophic strata can be easily recognized, life forms inventoried, their energy regime measured, and efficiencies calculated.

The Truelove Lowland ecosystem is one in a series of coastal lowlands on Devon Island and was chosen as the experimental study site for the Canadian IBP-Tundra Biome Study (Bliss 1972a). It offers a variety of life forms, is limited in size and therefore definable, but nevertheless large enough to sustain the impact of a larger group of investigators. The existence of the Arctic Institute of North America base camp and the possibility of aircraft transportation as well as the icebreaker logistic supply were practical factors.

Regular scientific activity in the Truelove Lowland and its

adjacent areas was initiated in 1960 when the base camp was established. Since then numerous studies have been conducted in Geology (Cowie 1961, Krupicka 1973), Periglacial Geomorphology (King 1969, Barr 1971) and Meteorology (Gill 1963). Before the IBP Devon Island project started, the biological disciplines had been represented mainly by Hussell (1972), Barrett (1972), and Teeri (1972).

The objectives of this study were to:

1. Determine plant communities and their standing crop in the three recognized zones of raised beaches and determine the seasonal (annual) increment in both above and below-ground production.

2. Compare the production of these beach ridge Polar Semi-desert vascular plant communities with that of lowland meadows (the lusher end of the lowland series) and that of the true Polar Desert on the upland plateau which surrounds the lowland (the most severe end).

3. Contribute to an understanding of primary production and decomposition processes in a cushion plant by studying plant phenology, adaptive and survival strategy, formation, storage, and translocation of carbohydrates, and plant structure via leaf angles, leaf area and chlorophyll in three main species, especially in *Dryas integrifolia*.

PHYSICAL ENVIRONMENT OF THE TRUELOVE LOWLAND

Description of Studied Area

Devon Island, N.W.T. (75°N) is the second largest island (ca. 54,000 km^2) in the Queen Elizabeth Islands. These high arctic islands are located north of 73°N latitude and extend beyond the 85°N parallel. Together with a southern group of islands they form the Canadian Arctic Archipelago and collectively comprise the High Arctic. Taylor (1956) described the physiography of Devon Island, especially the coastal areas and provided the historical review of the island's discovery.

Devon together with Ellesmere and Axel Heiberg Islands in the north and Baffin Island in the south, form the eastern edge of the Canadian Archipelago, and Devon shares with these islands a rather severe climate. These islands are also still partially ice covered.

The eastern highlands of Devon Island are covered by an ice cap (16,240 km^2) with a 1859 m high summit (Sharp 1956). The remaining upland is a barren Polar Desert formed of Silurian and Devonian formations (Taylor 1956). Plant and animal life is confined almost exclusively to coastal lowlands. The Truelove Lowland (75° 40'N, 84°33'W) is one of several along the northeast coast (Sverdrup - 26 km^2, Sparbo-Hardy - 86 km^2, Skogn - 13 km^2). Similar areas with a relatively lush vegetation and wildlife exist on other islands of the Canadian Arctic Archipelago. Although these areas comprise roughly only 3% of the ca. 400 thousand km^2 of the Canadian High Arctic, they are of basic importance for maintaining the life in these latitudes (Bliss 1972a).

The Truelove Lowland (43 km^2) is delineated by 24 km of shoreline on the west and north, by sedimentary (dolomitic) cliffs on the east and steep crystalline cliffs on the south (Fig. 1). It has three large

Figure 1. Location of study sites on the raised beaches and the plateau, Truelove Lowland.(▲)

lakes (933 ha.), and many small lakes and pools, interconnected in a drainage system emptying into the Truelove River or directly into Jones Sound. Raised beaches represent 20% (crest and slopes cover 294 ha, transitional zones 572 ha), meadows account for ca. 41% and rock outcrops for 12% of the entire lowland area.

The Truelove Lowland has partially developed from the Truelove River delta and is a part of an extensive coastal shelf strand flat. Although superglacial and periglacial streams do not presently carry as much meltwater as in the past, flow of the Truelove River is still large because of the nearby ice cap. There is no doubt that the enormous ice cap as well as the ice of Jones Sound which remains frozen most of the growing season, influence the climate of the adjacent areas (King 1969). The presence of ice is thus of ecological significance, and is only a matter of opinion as to whether the Ice Age has really ended here.

Post Wisconsin History

The western part of the Canadian Archipelago was deglaciated relatively early. Although the eastern part of Devon Island is still covered by an ice cap, Andrews (1970) estimated that the major part of the island was deglaciated 8700 years ago. The 8000 year BP isochrone (ice marginal timeline of presumed Wisconsin ice retreat) runs close to the northern coast of the island (Fig. 2). Ice retreat was followed by a significant isostatic rebound of the northern parts of the American and Eurasian continents. Andrews (1970) estimated that on Devon Island total postglacial uplift* was 91 m, averaging 1.4 m/100 years,

*The glacio-isostatic recovery and eustatic sea level changes have been (partially) self-cancelling (i.e. both were in the same direction). Postglacial uplift is computed as the amount of glacial emergence at specific times less the eustatic sea level at those times measured from present sea level (Andrews *et al.*, 1971).

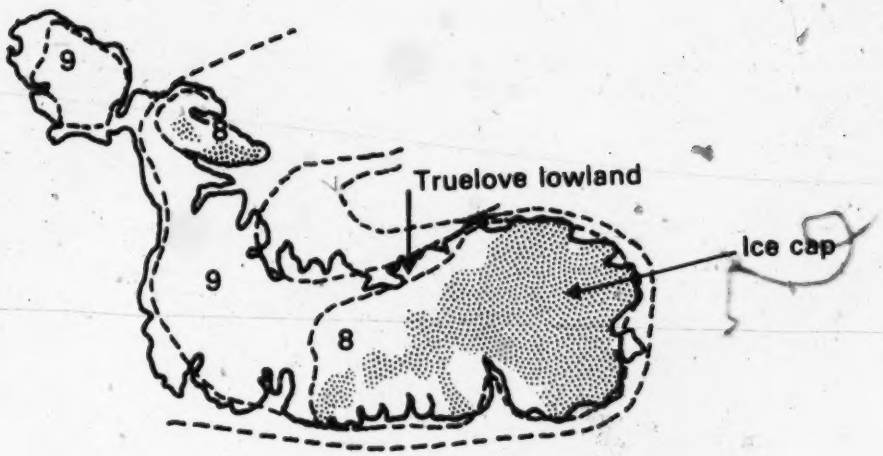

Figure 2. Deglaciation isochrones in thousands of years BP for Devon Island, redrawn from the Wisconsin and recent ice map of North Americ (Geol. Survey Can. Map 1275 A).

Figure 3. Formation of a new raised beach ridge in the Truelove Lowland.

with the present rate being 0.36 m/100 years.

Recently King (1969) and Barr (1971) presented evidence that in the Truelove Lowland the uplifted marine limits lie at 76 m above sea level and date approximately 9450 B.P., which is also considered to be the date of deglaciation. According to Barr (1971) today's postglacial uplift appears to be matched by eustatic sea level rise. The formation of a new beach ridge at the shoreline can be seen in Fig. 3, and Fig. 1 shows the sequence of beach ridges across the Lowland.

Geology and Geomorphology

King (1969) presented extensive information about bedrock geology, landscape development and Pleistocene phenomena of the Truelove Lowland.

A detailed petrological study of the crystalline rocks on the Truelove Lowland was done by Krupicka (1973). According to his findings all rocks forming the basement are metamorphic, the main rock types being granulites and gneisses. In this area the Canadian Shield is formed of Archean rocks "partially reworked and metamorphosed in the Lower Proterozoic".

The boundary horizon between the crystalline basement and the dolomitic sediments overlying it is formed by a thin quartz sandstone, fragmented on the exposed surface by strong frost activity. Except for the area of Rocky Point (Fig. 1) which is dolomitic, all other lowland areas of rock outcrops are crystalline and were smoothed on the surface by previous glaciation.

The predominant part of the lowland is covered by a Pleistocene mixture of crystalline, sandstone and dolomitic components reflecting the lithology of the nearest substrate and varying in the degree of

weathering. Summer temperature fluctuations around the freezing point have been responsible for a variety of frost phenomena such as rock splitting, solifluction, patterned ground, congelifraction, congeliturbation and soil involutions.

The present lowland landscape is largely a relic of the previous strong landforming processes that followed shortly after deglaciation and are almost absent at present (King 1969). From an ecological point of view, only water and wind erosion and their transporting role are significantly active processes now. It was observed by the author that after strong, warm, southern foehn winds, the black crystalline cliffs changed into a reddish color due to wind deposition of fine sedimentary material from the upper plateau.

Crystalline rock outcrops, flat depressional sedge meadows and raised beaches are the prevailing topographic features of the lowland in addition to lakes. Many meadows have developed on former lake bottoms as attested by their shallow gravel soils. Ice wedges and large polygons are common features both across and along raised beaches. As a result of more favorable temperature and moisture conditions in ice wedge furrows, there is a higher species diversity, and a greater standing crop and plant cover. This is responsible for the typical mosaic nature of the High Arctic (Khodachek 1969a, Aleksandrova 1971).

Raised beaches

A Beach Ridge is described as "A low, essentially continuous mound of beach-and-dune material (sand, gravel, shingle) heaped up by the action of waves and currents on the backshore of a beach beyond the present limit of storm waves or the reach of ordinary tides, and

occuring singly or as one of a series of approximately parallel deposits. The ridges are roughly parallel to the shoreline and represent successive positions of an advancing shoreline." (Glossary of Geology, Garry *et al.*, 1972).

Arctic raised beaches have been formed by ice push and tidal activity (Hume and Schalk 1964, Owens and McCann 1970), and their stepwise sequence across the lowland has followed the isostatic recovery after deglaciation. They are several hundred meters long and 30 to 150 m wide, frequently curved, and usually enclose a large depression with a meadow and one or more fresh-water lakes.

Raised beaches are formed of sand and gravel, the pebbles being mostly dolomite and crystalline material, locally sandstone. McCann and Owens (1969) found very little sand present on the beaches; most of the material falls into the pebble grade. Beach ridge sediments are moderately or poorly sorted due to absence of wave action for nine months of the year during time of formation.

In cross-section, a raised beach is a rounded convex body of a coarse material usually deposited on bedrock. The overall thickness varies but is often shallow (<1 m). A beach ridge starts as a distinct step (20-50 cm high) which indicates the "foot" of the ridge. On a typical beach ridge this part is flat and varies in width. In this study I shall refer to this part as the Transition Zone.

Behind the "foot" the fore-slope rises and is terminated by the rounded crest. Back-slopes are usually shorter and grade directly to a lake or a meadow. The slopes and crest are considered as separate ecological zones in this study (Fig. 4).

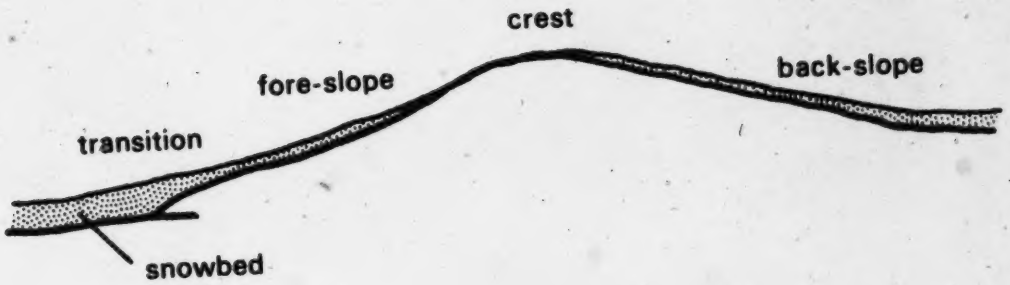

Figure 4. Profile of a raised beach. Meadows typically occur beyond the fore-slope and back-slope.

Frost activity has marked the ridges with deep (sometimes more up to 100 cm) ice-wedge type cracks (Fig. 5) running along and across them and dividing them into 15-80 m rectangles and polygons (Fig. 6). Except for the marginal shoreline area with recently formed beach ridges, ice wedges on the old uplifted ridges appear to be fossil and not expanding.

These ridges are one of the prevalent topographic features in arctic lowlands, they seem to be of great ecological significance. They are free of snow by mid-June while the adjacent meadows become snow-free 1-2 weeks later. Being relatively well-drained and exposed to the wind, they may be the driest and climatically most severe areas on the lowland, an ecological transition to the true Polar Desert on the upland plateau of the island. Raised beaches shield the adjacent meadows from wind (Courtin 1972), increase meadow snow cover by acting

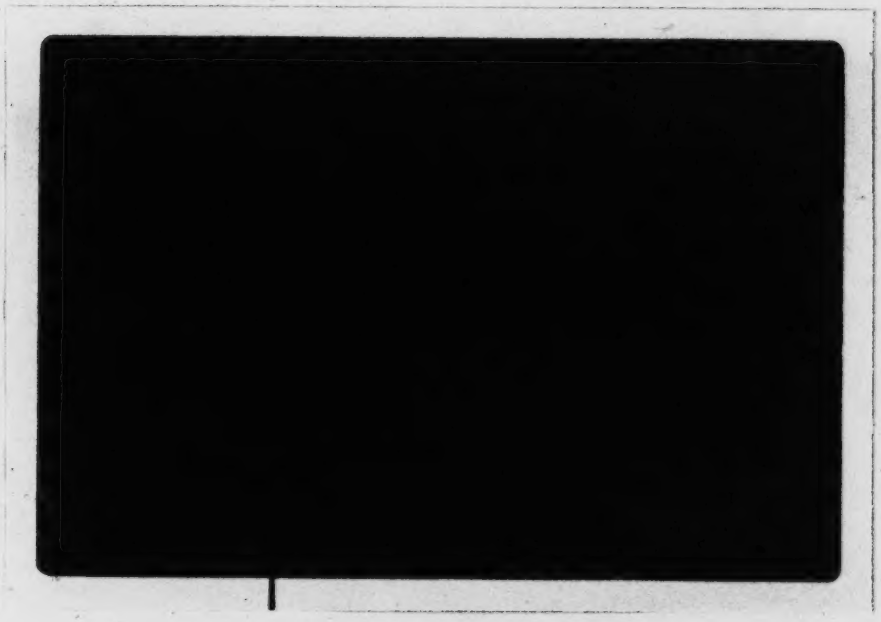

Figure 5. High arctic lowland. Pattern of raised beach ridges and meadows.

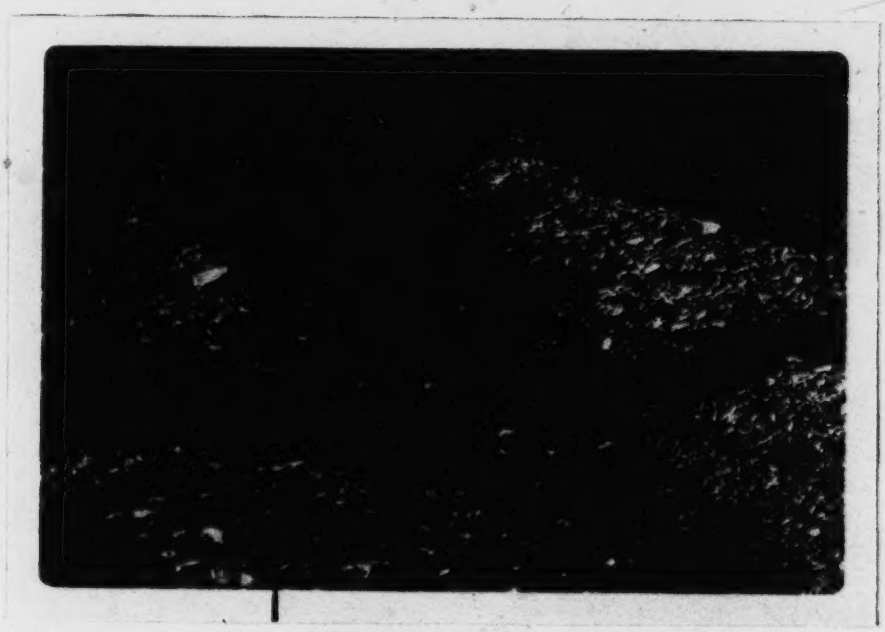

Figure 6. Fossile ice wedge running across a raised beach.

as natural barriers, and subsequently increase summer moisture of the whole meadow interzone. This creates more favorable conditions for many organisms and results in a special character of the lowland ecosystem.

Beside the typical and fully developed raised beach ridges, one can recognize several other topographic features in the lowland. Parallel to the main beach ridge and usually on its long foreslope less pronounced smaller terraces, the lower ridges often occur. This is the case of the relatively high raised beach chosen as an intensive study site by the Project (Fig. 7). Lower ridges do not always follow the curvature of the main beach ridge but sometimes separate from it and form long tongues. Between the main ridge and the tongues there usually develops a flat drainage depression. Flat, slightly bulging areas, sometimes considerable in size but without the pronounced beach ridge topography are distinguished from meadows as subdued ridges. When their ground surface is formed of larger boulders, such an area is referred to as a boulder pavement. When the composition of the fine substrate prevails, it indicates that the area has been subjected to strong frost activity and gave origin to a frost-boil subdued ridge.

Plateau

The Truelove Lowland is a marginal phenomenon compared to the vast geography of the Island's plateau, which rises sharply as a massive vertical escarpment 300-400 m above sea level, and represents a true polar desert. The inland plateau is characterized by its smooth topography interrupted only by a distinct drainage system. Here too a mosaic of variable patterned ground features covers the fragmented sedimentary rock surface.

Figure 7. The intensive study raised beach site (IRB) in the Truelove Lowland.

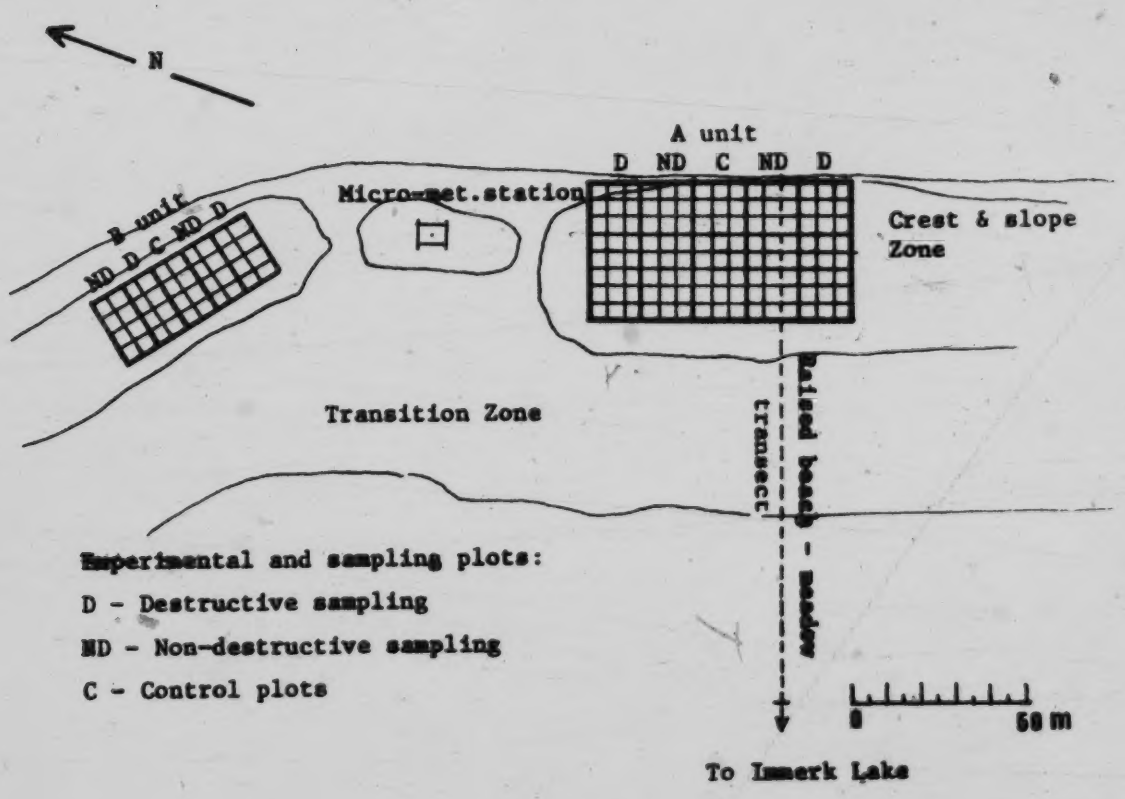

Figure 8. The design of the IBP Intensive Study Site on IRB.

Climate

Devon Island is dominated by a polar climate. The proximity of Jones Sound which is frozen for the major part of the year, and the presence of a near-by extensive ice cap are the decisive climatic factors in addition to the latitudinal position. At this latitude the polar night lasts from October 30 to February 11, the continuous arctic day from April 28 to August 14; both are periods of 108 days. In the lowland snowmelt begins in the middle of June and is delayed on the plateau 10 to 14 days.

King (1969) and Barrett (1972) believe that the Devon Island ice cap has an effect on the lowland climate and, in this way, also on the vegetation in the lowland because of the pronounced strong adiabatic winds, influenced by the nearby ice cap. The Canadian arctic islands contribute significantly to the world's pool of cold air (King 1969). The local temperature anomalies (compared with the theoretical mean for the latitude) are altogether negative. As Courtin (in Bliss *et al.*, 1973) pointed out, the fluctuation of radiation intensity (controlled by the cloudiness) can be correlated with the cyclonic activity in arctic regions. Also the periods of higher wind are associated with this cyclonic activity, which is higher with the progress of the season. Warmer air masses invade the area in summer as well as in winter, but their influence is limited. They are responsible, however, for frequent temperature inversions in the lowland and advection fogs resulting from them. Relative humidity near the ground is high during the entire growing season (85-95%).

Vowinkel and Orving's (1970) data show that the mean cloud cover for this latitude increases during summer months from 75 to 85%. It

decreases, however, progessively in September and October to 50%, and is maintained at this level until April. This is supported by Courtin's 1971 and 1972 measurements in the lowland, with further qualification that even lower cloudiness in fall may cause greater reduction of total radiation due to lower angle of radiation incidence. In Truelove Lowland the theoretical solar flux for this latitude was reduced to 50-60% during June and July but oscillated between 28-75% in August and September. According to King (1969) the real number of sunshing hours represented only 32% in 1961 and 35% in 1962 in Truelove Lowland.

Three well equipped meteorological stations were established by Courtin at the AINA Base camp, and at the intensive study sites on the Experimental Ridge and Experimental Meadow. Several other small meteorological units were distributed on significant sites of the lowland and the East Plateau. The cloud and fog screening effect shows even more clearly from the figures of incoming total radiation recorded by Courtin (Fig. 9a). In 1970, 1971 and 1972 mean weekly temperatures of the Base Camp raised beach reflect the radition intensity of the lowland (Fig. 9a) and are presented in Fig. 9b. These figures also show the range of the potential growing season in three consecutive years recorded.

Data collected in the summer of 1970, 1971 and 1972 were computerized and are synthetized in the IBP Reports by Courtin (1972, 1973). There has been a continuation of meteorological measurements throughout the winter of 1972-73. This synthesis will be presented by Courtin in the final report.

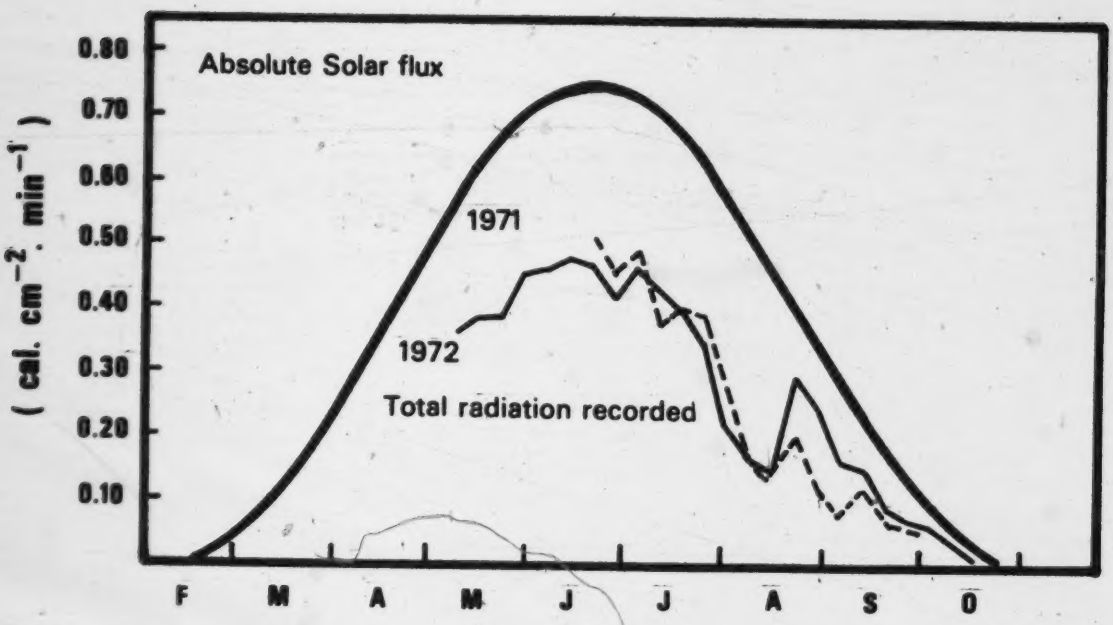

Figure 9a. Absolute solar flux (daily means) for Devon Island (75.66°N, 84.66°W), and the total radiation (weekly means) recorded in the Truelove Lowland in summers 1971 and 1972 (calculated and compiled from Courtin 1971 and 1972 data).

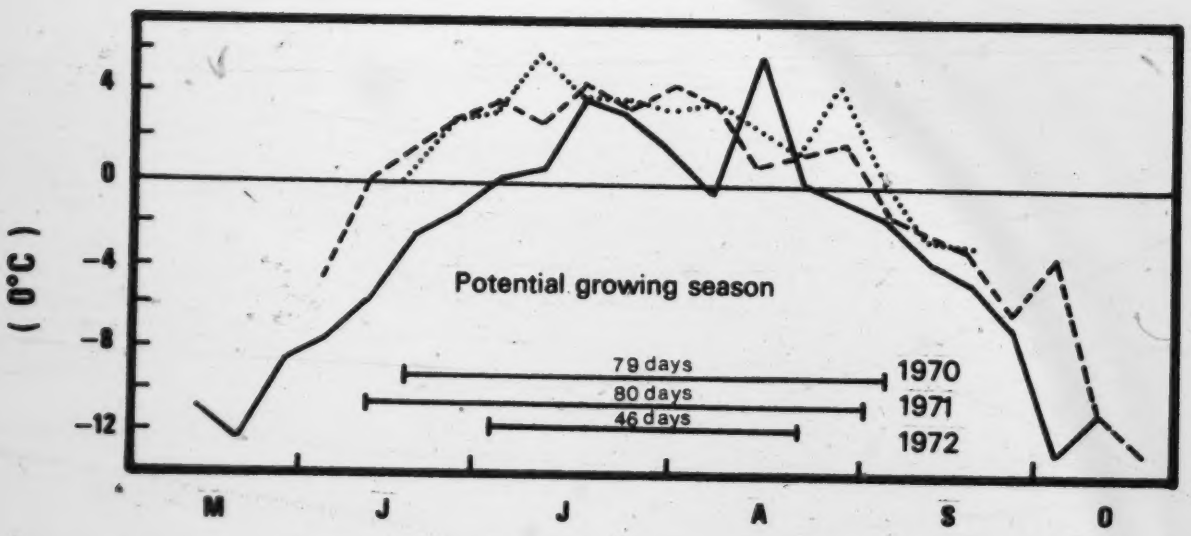

Figure 9b. Base Camp raised beach weekly mean temperatures at 1.5 m in summer 1970, 1971 and 1972 (reworked from Courtin 1973).

METHODS, RESULTS AND DISCUSSION

General Notes

Intensive study site

In early June, 1970, two large areas (units) were established for permanent studies on a raised beach, called "Intensive Raised Beach" (IRB), elevation 28 m, age 7500 years, east of Immerk Lake. These units (40 x 75 m and 20 x 50 m) were subdivided into Destructive, Non-destructive and Control plots. Each plot was further subdivided into 5 x 5 m subplots where the actual "intensive program" has been performed (Fig. 7 and 8).

Extensive study sites

An extensive study was conducted on eleven raised beaches and at two neighboring areas A and B on the plateau (Fig. 1). Plant cover and standing crop data were related to the age and elevation of the beach ridges.

Soils

The first attempts to characterize Polar Desert Soils are associated with Russian authors, e.g., Gerasimov (1956) and Svatkov (1961). Actual soil descriptions have been presented by Tedrow and Douglas (1964), Tedrow (1966), Charlier (1969) and Cruickshank (1971).

Tedrow and Douglas (1964) define Polar Desert Soils as "those mature well drained soils of the High Arctic having a sparse (≤25%) covering of higher plants". July temperature does not exceed 4.5°C and precipitation is very low (50-75 mm).

Although the Truelove Lowland falls within such a climatic zone,

the true Polar Desert soil is only to be found on the plateau surrounding the lowland. Raised beaches, some rock outcrop areas with highly disintegrated and weathered surfaces, and the base of the escarpment however contain soils very similar to those types described by the above authors. The irregular character of these particular landforms supports the development of various soil and plant community continuua and transition areas with different drainage, winter snow depth and plant cover. Soil development occurred in relation to these biophysical microsites, and as a result a mosaic of closely related or totally unrelated soil types developed. They range from light colored Polar Desert-like soils on some crests to soils relatively rich in dark organic matter in some parts of the transition.

The intermediate character of these raised terraces expressed by various microclimatic, vegetational and soil gradients can be best classified as Polar Semi-desert (Bliss *et al.*,1973).

In the Truelove Lowland, King (1969) studied pedogenesis in relation to plant cover. King collected analytical data on soil profiles and completed a crude soil map of the Lowland. Both authors have applied Tedrow's concept of Polar Desert Soil to the raised beaches.

Peters and Walker (1972) and Walker (1973) have found more soil development on the Lowland raised beaches than is characteristic of Polar Desert Soils. On the Intensive Raised Beach the very top of the Crest Zone contains "regosolic-like" soil, dark greyish-brown with gravelly, coarse sand in the Ah horizon (pH 7.8) and low organic matter content.

In flat areas surrounding these narrow regosolic strips, soil development has progressed further. More vegetation is present and

"Brunisolic-like" (Arctic Brown) soils are found. These are dark brown, with plentiful very fine and fine roots in the Ah horizon (top 10 cm); pH is 7.8. A dark greyish-brown Bm horizon (10-20 cm) can be distinguished.

The margins of IRB, as well as some depressions in the Transition Zone, contain Gleysolic soil (Tundra Soils). A very dark brown of horizon (top 15-25 cm) and fibrous organic matter are characteristic of these soils. A bluish-grey clay band is present just below the organic matter. Peters and Walker (1972) have also provided chemical and physical characteristics for most of the soil profiles described.

Methods

In 1970 soil samples were collected on a 150 m long east-west transect across the IRB which encompasses all three beach ridge zones and part of the adjacent meadow. The samples were collected in 0-10 cm and 10-20 cm depth, each layer in duplicate. The same year another set of soil samples was collected from the 30 cm deep soil profile on the crest of the IRB and one surface sample on the Plateau. Chemical and mechanical analyses were done by the Soil and Feed Testing Laboratory, Alberta Department of Agriculture, Edmonton.

Results and Discussion

Table 1 presents the results of chemical and mechanical analyses of the IRB soil profile. There is a very low available nutrient status in these soils. Organic matter and clay content are also very low.

Analyses of soil samples on the east-west transect (Table 2) do not show progressive changes in parameters except for the Crest Zone (8 to 30 m segment of a transect). Here figures are generally lower,

Table 1. Chemical and mechanical analysis of the soil profile on the crest, Intensive Raised Beach Site (IRB) and the Plateau, 1970. Analysed soil profile was described as Cryic Eutric Brunisol by Peters and Walker (1972).

Depth (cm)	Available nutrients (ppm) N	P	K	NA	pH	Conductivity (%)	SO_4 (%)	Organic Matter (%)
Crest								
0- 5	0.5	3.0	53	0	7.8	0.20	1.2	3.70
5-10	1.0	0.0	23	5	8.0	0.20	0.0	1.41
10-15	0.0	0.0	7	20	8.4	0.10	0.0	0.24
15-20	0.5	0.5	6	0	8.3	0.10	0.0	0.43
20-25	0.0	1.0	8	25	8.3	0.10	0.0	0.29
25-30	0.0	5.5	4	0	8.4	0.10	0.0	0.15
Plateau	1.0	1.5	56	15	8.3	0.30	5.0	1.67

Depth (cm)	Hygroxc. Moisture (%)	N total (%)	Organic carbon (%)	$CaCO_3$ (%)	C/N	Base sat. (%)	Sa*	Si	Cl	Fi cl	Texture
							-- % --				
Crest											
0- 5	0.95	0.20	2.15	6.40	11	100	94	1	5	0	sand
5-10	0.47	0.05	0.82	9.69	16	100	88	3	9	0	sand
10-15	0.15	0.01	0.14	10.49	14	100	88	3	9	.7	sand
15-20	0.22	0.02	0.25	9.06	13	100	95	2	3	.7	sand
20-25	0.22	0.02	0.97	9.55	9	100	96	1	3	0	sand
25-30	0.13	0.01	0.09	10.97	9	100	93	2	5	.2	sand
Plateau	0.55	0.11	0.97	36.90	9	100	36	32	32	1.3	clay loam

*Sa=sand, Si=silt, Cl-clay, Fi cl = fine clay

Table 2. Chemical and mechanical analysis of the soils along the transect Intensive Raised Beach - Frost boil-sedge-cottongrass meadow

A.

Transect (m)	Depth (cm)	Available nutrients (ppm) N	P	K	Na	pH	Conductivity (%)	SO_4 (%)
Backslope transition:								
0	0-10	2.7	11.7	106	27	6.0	0.15	13.5
	10-20	0.5	5.0	25	5	6.1	0.20	7.6
Crest:								
8	0-10	1.7	4.2	65	7	7.6	0.30	4.3
	10-20	0.6	6.5	29	0	8.0	0.15	2.4
20	0-10	0.5	6.4	54	2	7.7	0.20	2.4
	10-20	0.5	4.7	48	2	8.2	0.20	1.8
30	0-10	1.7	4.2	40	0	7.9	0.15	1.8
	10-20	0.7	5.0	20	0	8.1	0.10	0.0
Slope:								
40	0-10	0.7	3.2	23	5	8.1	0.10	1.2
	10-20	0.5	3.0	15	2	8.1	0.10	0.6
50	0-10	0.5	6.7	34	17	7.7	0.30	5.0
	10-20	0.5	2.5	14	15	7.8	0.20	1.2
Transition:								
60	0-10	2.0	4.2	45	10	7.7	0.25	3.7
	10-20	0.7	2.0	18	20	7.9	0.15	1.2
75	0-10	1.5	3.2	31	15	7.6	0.25	4.2
	10-20	0.5	2.2	13	10	8.0	0.10	1.5
82	0-10	1.5	2.2	27	27	7.2	0.20	7.7
	10-20	1.7	1.2	21	20	7.3	0.20	6.5
90	0-10	1.0	3.7	57	20	7.6	0.20	5.0
	10-20	0.7	2.5	18	15	8.0	0.15	1.2
100	0-10	0.7	4.7	28	10	7.6	0.25	5.9
	10-20	0.5	3.2	13	15	7.9	0.20	1.8
Meadow:								
125	0-10	1.0	3.2	28	20	7.3	0.20	3.6
	10-20	0.5	5.7	29	10	7.6	0.20	3.0
135	0-10	1.2	4.7	44	10	7.3	0.20	4.3
	10-20	0.5	2.7	19	25	7.8	0.20	2.4
140	0-10	0.7	6.0	105	20	7.4	0.20	11.0
	10-20	0.0	5.4	66	10	7.9	0.20	1.2
150	0-10	0.5	1.2	61	25	7.8	0.30	5.3
	10-20	0.5	0.0	56	12	7.9	0.10	7.0

B. (Table 2 cont'd)

Transect (m)	Depth (cm)	Hygroscopic moisture (%)	N total (%)	Organic matter (%)	Organic carbon (%)	$CaCo_3$ (%)	C/N
Backslope transition :							
	0-10	7.20	2.13	47.45	27.59	-	13
0	10-20	1.71	0.53	0.05	5.26	-	10
Crest:							
8	0-10	1.54	0.44	8.02	4.66	3.01	11
	10-20	0.51	0.11	2.16	1.25	6.90	11
20	0-10	0.34	0.11	2.05	1.79	1.03	10.5
	10-20	0.26	0.06	0.76	0.44	6.30	7
30	0-10	0.68	0.20	1.77	1.03	6.30	5.5
	10-20	0.41	0.07	1.17	0.68	9.14	9
Slope:							
40	0-10	0.52	0.12	1.64	0.95	8.24	8
	10-20	0.34	0.07	0.96	0.56	9.28	7.5
50	0-10	2.03	0.44	10.22	5.94	4.85	13.5
	10-20	1.46	0.22	6.59	3.83	5.72	19.5
Transition:							
	0-10	1.69	0.43	7.43	4.32	4.21	10
60	10-20	1.12	0.22	4.49	2.61	7.38	12
75	0-10	1.23	0.29	6.32	3.67	1.71	13
	10-20	0.42	0.07	1.61	0.93	6.43	13.5
82	0-10	1.99	0.26	10.27	5.97	2.42	12.2
	10-20	2.29	0.54	11.48	6.67	1.54	12.5
90	0-10	1.31	0.36	7.41	4.31	1.58	11.5
	10-20	1.17	0.17	3.99	2.32	7.98	14.5
100	0-10	1.23	0.30	4.78	2.78	3.30	9
	10-20	1.50	0.24	5.11	2.97	2.94	12.5
Meadow:							
125	0-10	2.28	0.50	10.23	5.95	3.45	12.5
	10-20	1.41	0.34	6.66	3.87	2.43	11.5
135	0-10	1.94	0.39	9.80	5.71	3.20	16
	10-20	0.64	0.13	2.70	1.57	5.49	12
140	0-10	2.00	0.51	9.46	5.50	7.74	10.5
	10-20	0.95	0.24	4.05	2.36	7.22	10
150	0-10	0.51	0.12	2.56	1.49	8.89	12
	10-20	0.31	0.04	0.73	0.42	19.86	9.5

C. (Table 2 cont'd)

Transect (m)	Depth (cm)	Exchangeable cations milliequivalent/100 grams H	Na	K	Ca	Mg	Total	Total exch. capac.	sat. (%)	Mechanical analysis Sand ---	Silt %	Clay ---	Fine Clay	Texture
Backslope transition:														
0	0-10	9.45	.47	.61	46.67	11.56	68.77	76.59	77					
	10-20	4.16	.12	.05	11.41	2.74	18.48	19.79	81	88	8	3	1	loamy sand
8	0-10		.22	.17	24.06	9.34	33.79	28.72	100	85	12	2	1	loamy sand
	10-20								100	90	8	2	.2	loamy sand
20	0-10								100	93	6	.4	.3	sand
	10-20								100	92	5	2	.8	sand
30	0-10		.05	.12	11.82	2.90	14.89	14.20	100	94	4	.9	.6	sand
	10-20								100	92	7	.7	.0	sand
Slope:														
40	0-10													
	10-20								100	94	5	.8	.5	sand
50	0-10								100	90	10	.2	.1	sand
	10-20								100	90	2	8	0	sand
Transition:									100	91	4	5	0	sand
60	0-10													
	10-20								100	86	9	5	0	loamy sand
75	0-10		.10	.07	15.01	3.93	19.12	15.69	100	82	11	7	0	loamy sand
	10-20								100	92	4	3	0	sand
82	0-10	2.30	.13	.07	25.45	6.67	34.65	32.14	100	93	3	4	0	sand
	10-20		.10	.06	27.72	7.19	35.07	35.09	93	80	16	4	2	loamy sand
90	0-10		.11	.15	16.88	4.96	22.09	21.96	100	80	16	3	2	loamy sand
	10-20								100	85	11	4	2	loamy sand
100	0-10		.59	.06	14.29	4.07	19.02	15.94	100	88	8	4	2	sand
	10-20								100	99	5	3	1	sand
Meadow:									100	87	9	3	2	sand
125	0-10		.58	.08	22.87	7.23	31.68	30.37	97	91	8	1.4	.6	sand
	10-20		.49	.05	16.28	5.79	24.11	22.96	100	89	7	4	.8	sand
135	0-10		.11	.10	16.75	5.25	22.22	22.28	100	96	1	4	.2	sand
	10-20								100	89	7	3	.3	sand
140	0-10		.21	.14	22.38	6.96	29.69	27.34	100	86	12	2.2	1.1	loamy sand
	10-20								100	90	7	3	1	sand
150	0-10		.08	.07	11.61	1.63	13.39	9.23	100	76	8	16	2	loamy sand
	10-20								100	65	22	12	.2	sandy loam

exchangeable cations have almost no measurable level. Significant are differences between the surface (0-10 cm) and subsurface soil (10-20 cm). The upper soil is richer in organic matter, total nitrogen, and some other characteristics. On the contrary pH increases with depth.

Soil analyses did not fully support expected differences in nutrient status along the beach ridge-meadow transect. The beach ridge seems to be a geochemically fairly homogenous unit where today's plant cover and species composition are still conditioned more microclimatically (possibly by available moisture) rather than by differences in soil substrate. Where the microclimate has been more favorable and a denser plant cover could develop, soils are slightly more developed. According to King (1969) there is only a slight differentiation in various beach ridge soils in spite of their marked differences in age. This suggests that there was a long vegetational delay which followed deglaciation or a very slow start in the early phase of plant establishment.

Microclimate

Radiation, active layer, and soil and plant temperature

Methods

Active layer development was measured using a calibrated steel rod. Within the experimental area, active layer was measured along a transect (1 m interval) every two or three days during the thaw period, and once a week during refreeze. Active layer depth along the IRB-meadow transect line was measured at topographically significant points once a week. Temperature measurements (thermocouples) were made twice a week in a profile (25, 3, 0, -5, -15 and -25 cm) on three permanently

established microclimatic stations one in each of the zones. Plant temperatures were measured by thermocouples introduced into the center of a plant clump.

Snow depth observations have been made on permanently fixed graduated wooden rods, located in an EW transect across the IRB, at points established for the measurement of active layer. Snow depth was measured every two or three days until snow disappearance. Snow density samples were collected in 3 replicates every second day during the thaw period.

Samples for soil moisture content (n = 4, gravimetric method) were regularly collected during the entire growing season. Sampling pattern was similar to other microclimate measurements described above.

Results and discussion

Radiation: Data for 1971 and 1972 (Fig. 9) show that over the lowland there is a decrease of total incoming radiation from the end of June (0.5 cal. cm^{-2}. min^{-1}) to the end of September (0.05 cal. cm^{-2}. min^{-1}). Net radiation for the Intensive Raised Beach was estimated to be 1.55 x 10^8 cal.m^{-2}. Total incoming radiation (Rt) for the same period was 3.42 x 10^8 cal.m^{-2}. The ratio of R_n/R_t = 0.45, in other words approximately 45% of the total incoming radiation reached the ground and was absorbed.

Active layer: The lowland is underlain by very deep and cold permafrost (Brown 1972). On the crest of raised beaches the active layer reaches a maximum of 75-100 cm but is shallower (40-70 cm) on the slopes and the transition to meadows. After snowmelt the active layer develops rapidly, reaching maximum depth in 30 to 40 days. The first few days

after snowmelt the active layer is still shallow and the surface temperature of the ground is significantly influenced by the permafrost table. Once the permafrost table lowers, its influence weakens and the actual surface temperature is dominated mainly by current climatic factors, especially by radiation. However, the root zone is influenced by the permafrost table for a much longer period.

Soil and plant temperature: Courtin (1972) found a gradual temperature difference across the lowland from the top of the plateau to the coast (7.3°C) at the beginning of July 1971. These differences, measured at six stations and based on weekly means, was maintained during the main portion of the 1971 growing season and suggests that the microclimatically most favored sites are distributed inland from the coast, the rock outcrops and the base of the cliffs.

Courtin and to a lesser extent the author, measured a vertical temperature profile on the Intensive Raised Beach throughout the growing seasons of 1971 and 1972. A distinct vertical temperature profile exists with the highest temperature being near the surface. Figure 10 illustrates temperature gradients on the slope and the crest measured on sunny days (July 27 and August 3, 1971). Plant temperature inside the clump was measured in three species.

Plant clump temperatures are close to ambient air temperatures in the first 3 cm above the surface, are significantly higher than the air at 25 cm (Fig. 10). This suggests that a favorable thermal microclimate exists near the ground on the ridges and partially explains why the high arctic species have not developed higher vertical structure. Leaves of these cusion plants may, however, exceed 10 to 15°C the ambient air temperatures (Addison 1973).

Marked differences between ambient and plant temperatures were recorded also by Tikhomirov *et al.*, (1960) at Yakutsk (71°, 35'N), USSR and Warren Wilson (1957) at Resolute Bay, Cornwallis Island.

Measurements in 1972 showed that at the IRB the temperatures near the ground were regularly 2-5°C higher on the crest compared with those on the slope, because of exposure angle to incident radiation.

Figure 11 shows the overall seasonal distribution of vertical temperature in 1971 (based upon Courtin 1972). Highest temperature at the surface occurred in late June, shortly after peak sun angle. After mid-July, temperatures decreased rapidly, except at -100 cm where peak temperature occurred two months later. Compared with the Intensive Meadow, 500 m distant, raised beach temperatures at the surface were almost 4°C higher (Courtin 1972).

On August 9, 1972, a continuous series of hourly microclimatical measurements were conducted in all three zones. The stations were 30 and 40 m apart; the Crest Zone station was 3 m higher than that in the Transition Zone. The weather gradually changed from a relatively sunny first day to cloudy and rainy weather during the second day. Profile temperatures followed the changing weather conditions (Fig. 12). At the beginning there were marked differences between zones, especially in soil temperatures. Under continuously cloudy and rainy weather the differences slowly disappeared and the microclimate profiles were rather similar in all three zones. Figure 13 shows the zonal differences in temperature for the 3, 0 and -5 cm positions. Temperatures were highest in the boundary layer, the same location as the plants. Ecologically meaningful is the finding, that during sunny periods surface temperatures are higher on the crest, while during cloudy and rainy weather the slope

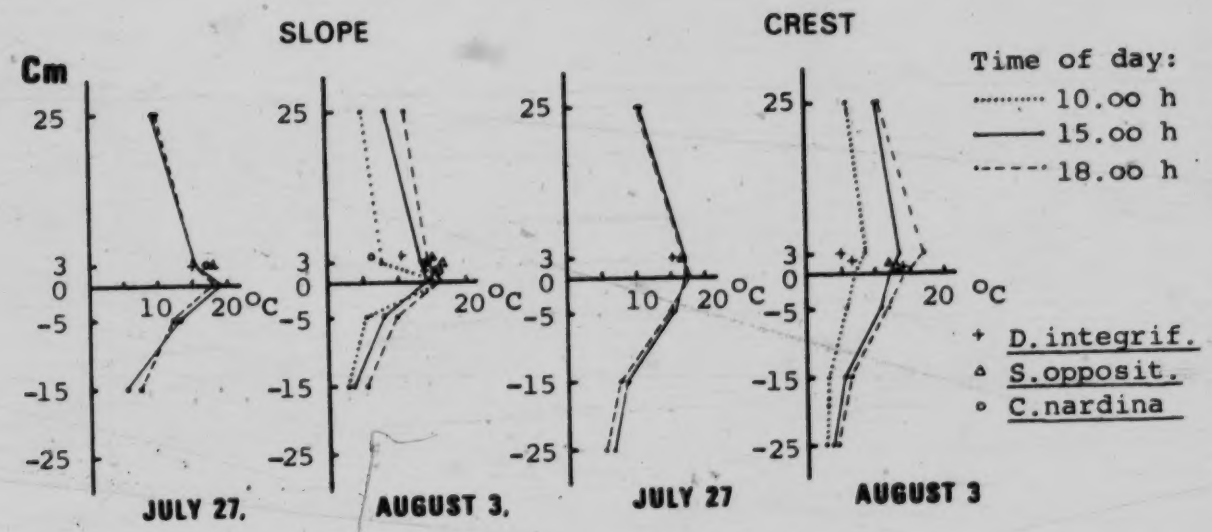

Figure 10. Temperature profiles on the Intensive Raised Beach on two sunny days in summer (1971).

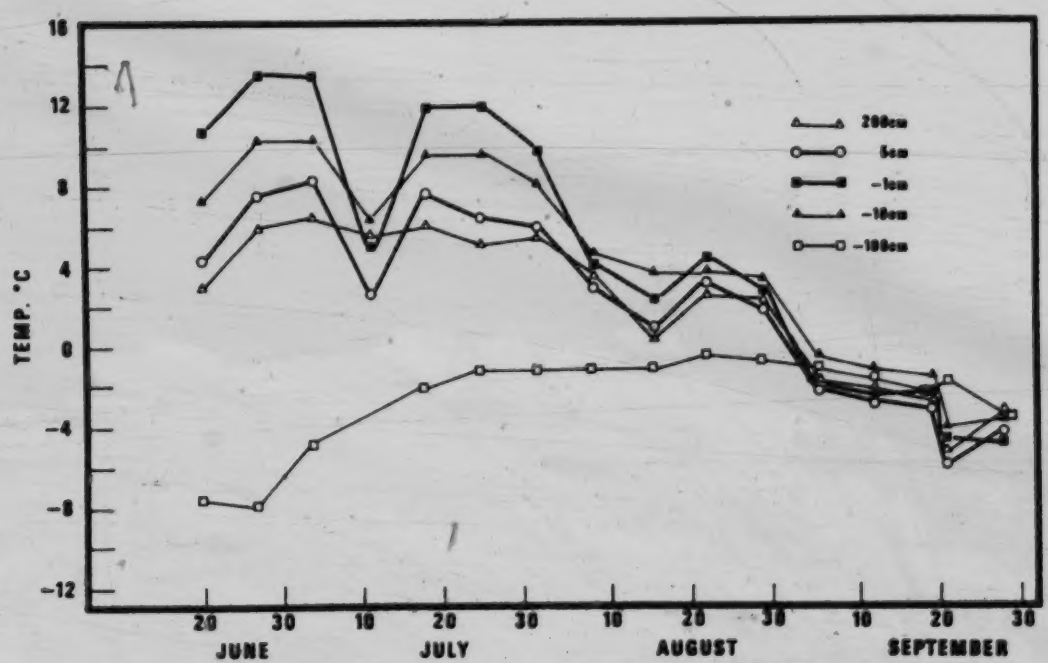

Figure 11. Temperature profile on the crest of IRB in summer 1971 (after Courtin 1972).

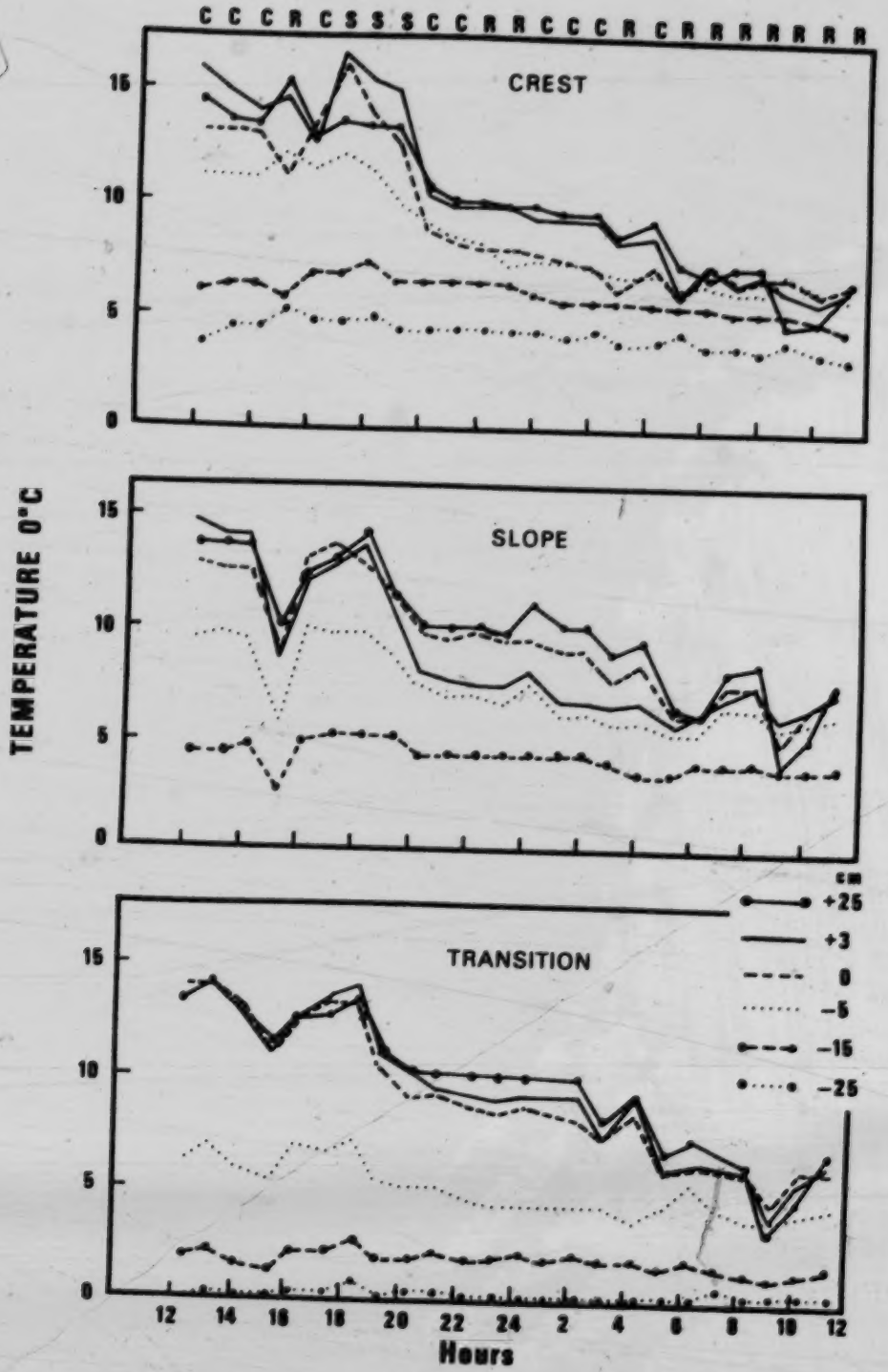

Figure 12. Temperature profile in three zones of IRB during changing weather on August 9 and 10, 1972. Weather synbols are: C (cloudy), R (rainy), S (sunny).

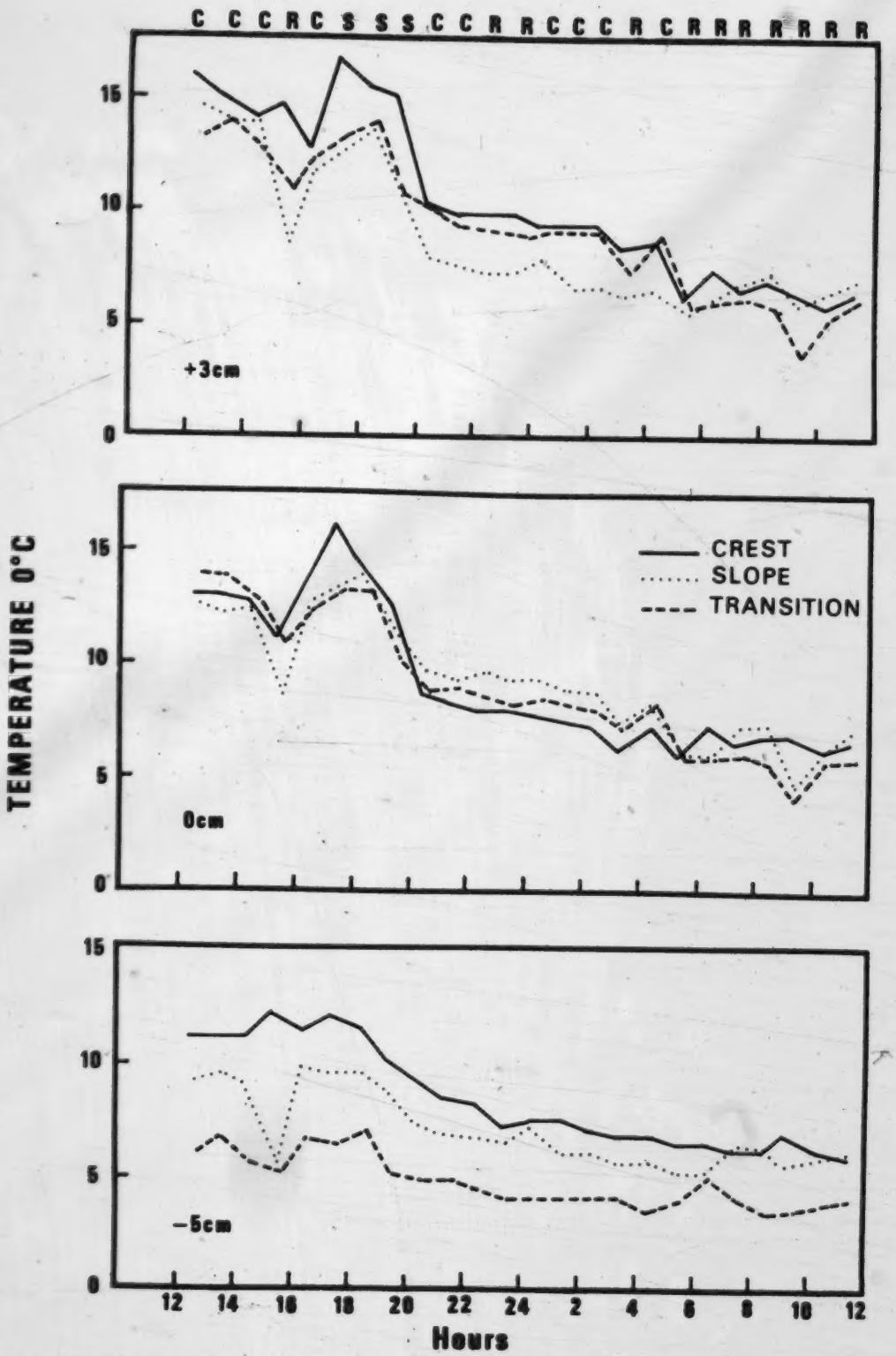

Figure 13. Temperatures near the ground in three zones of IRB during the changing weather on August 9 and 10, 1972. Weather symbols are: C (cloudy), R (rainy), S (sunny).

is slightly warmer due to shielding against the wind. Soil (-5 cm) temperatures show the most distinct differences between zones. The lower temperature itself does not seem to be as ecologically harmful as is the occasional temperature raise (crest) which causes high respiration and fluctuation in available moisture (Addison 1973). There is also evidence of a slight temperature inversion between the surface and 25 cm during the rainy period, undoubtedly caused by the low soil temperatures (Fig. 12).

Wind, precipitation and soil moisture

Wind: In 1971 weekly mean wind velocities (25 cm) ranged between 1.15-3.54 m/sec, with the mean seasonal velocity being 2.16 m/sec, while the Intensive Meadow experienced a mean seasonal wind velocity of only 1.67 m/sec (Courtin 1972). Generally speaking, wind velocities increase with the progress of the season, the highest velocities occurring in late Autumn. The sudden strong adiabatic winds, foehns, which may occur two or three times during the growing season are probably significant but their effects on the lowland ecosystem are not well documented.

Precipitation and soil moisture: Due to interactions of wind and topography, snow is blown from the crest and deposited in the lee side of the ridge. Table 3 shows snow cover in the early part of the growing season.

Table 3. Snow cover (cm) on the Intensive Raised Beach, Spring 1971

Date	Crest (cm)	Fore-Slope (cm)	Transition (Snowbed) (cm)
June 17	0-5	10	56
June 20	0	5	50
June 24	0	0	32
June 28	0	0	10
July 1	0	0	0

By the end of June snow disappears rapidly from the crests and slopes, but persists for a longer period of time in the transitional snowbeds. Figure 14 demonstrates the process of snowmelt, changes in snow density, active layer development, and soil moisture regime after the snowmelt and during the growing season. After snowmelt, crests are water saturated for a few hours, transition zones for several days.

Later in the season soil moisture varies with time, depth, soil type, and position on the beach ridge. The crest, as the earliest snow-free and best drained zone, maintains the lowest soil moisture throughout the season. The slope has a slightly higher moisture regime, but decreases in moisture content, especially near the end of the season. The transition starts off with saturated and virtually flooded soils, as is the case in meadows. During the first weeks after snowmelt the water slowly drains and soil moisture (determined on a volume basis) drops rapidly. At the end of the season soil moisture in the Transition exceeds 3 times that of the Slope and Crest Zones.

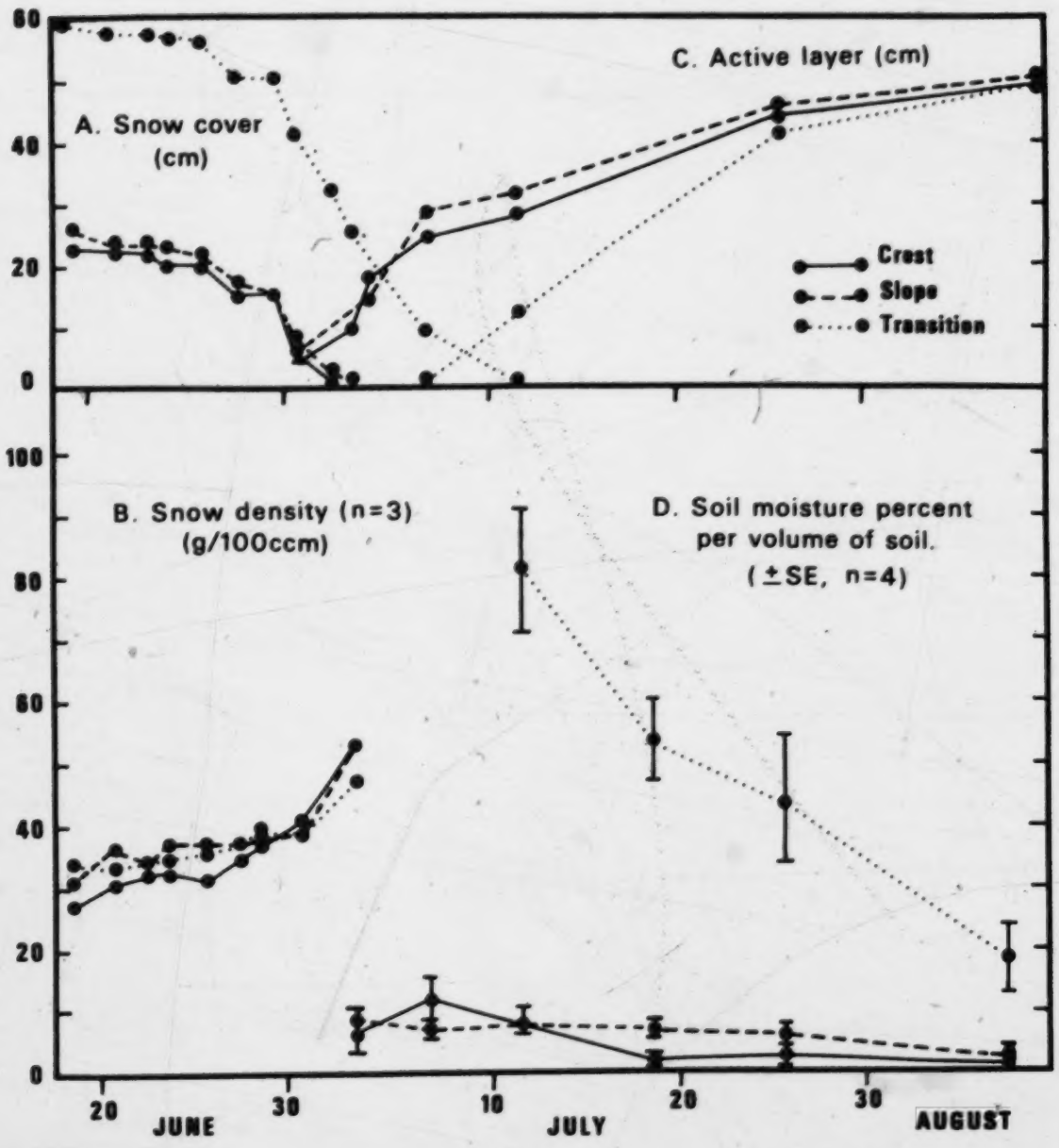

Figure 14. Snow cover (a), snow density (b), active layer (C) and soil moisture (D) in three zones of the Intensive Raised Beach in 1972.

Figure 15 shows the topographic profile of the IRB with the maximally developed active layer and soil moisture status at the end of the growing season (August 13, 1970). The initial delay in active layer development between the crest and the transition is overcome but the soil moisture across the ridge reflects the local drainage conditions, and slope orientation of the site for the whole summer.

Courtin (1973) gives precipitation values of 60, 62 and 47 mm over the four-month period during the summers 1970, 1971 and 1972 respectively. In 1971, July contributed only 13.7 mm of the total amount measured. Due to such low precipitation which is indeed characteristic for this latitude, the main source of water for this plant community is the melt water available at the beginning of the season. After this water is drained and evaporated, the plants are subjected to considerable water stresses. On IRB, Addison (1972) found that leaf water potential in living *Dryas integrifolia* plants can reach -35 bars. Teeri (1973) measured a field leaf water stress in *Saxifraga oppositifolia* of -44 bars without any apparent damage to the plants. There is no doubt that other plants in this community are exposed to similar water stresses and have the ability to survive under such conditions. This extremely low water potential gives evidence of the polar semi-desert to polar desert character of this community most eloquently. Relative humidity is very high (*ca.* 90%) during the entire season.

Plant Communities

From the days of the pioneers and explorers there has always been an interest in the high arctic flora. In recent times, Warming (1921), Sørensen (1941), Hadac (1941, 1963), Oosting (1948), Polunin (1948, 1959), Savile (1964, 1972), Aleksandrova (1961), Gavriliuk (1961, 1966),

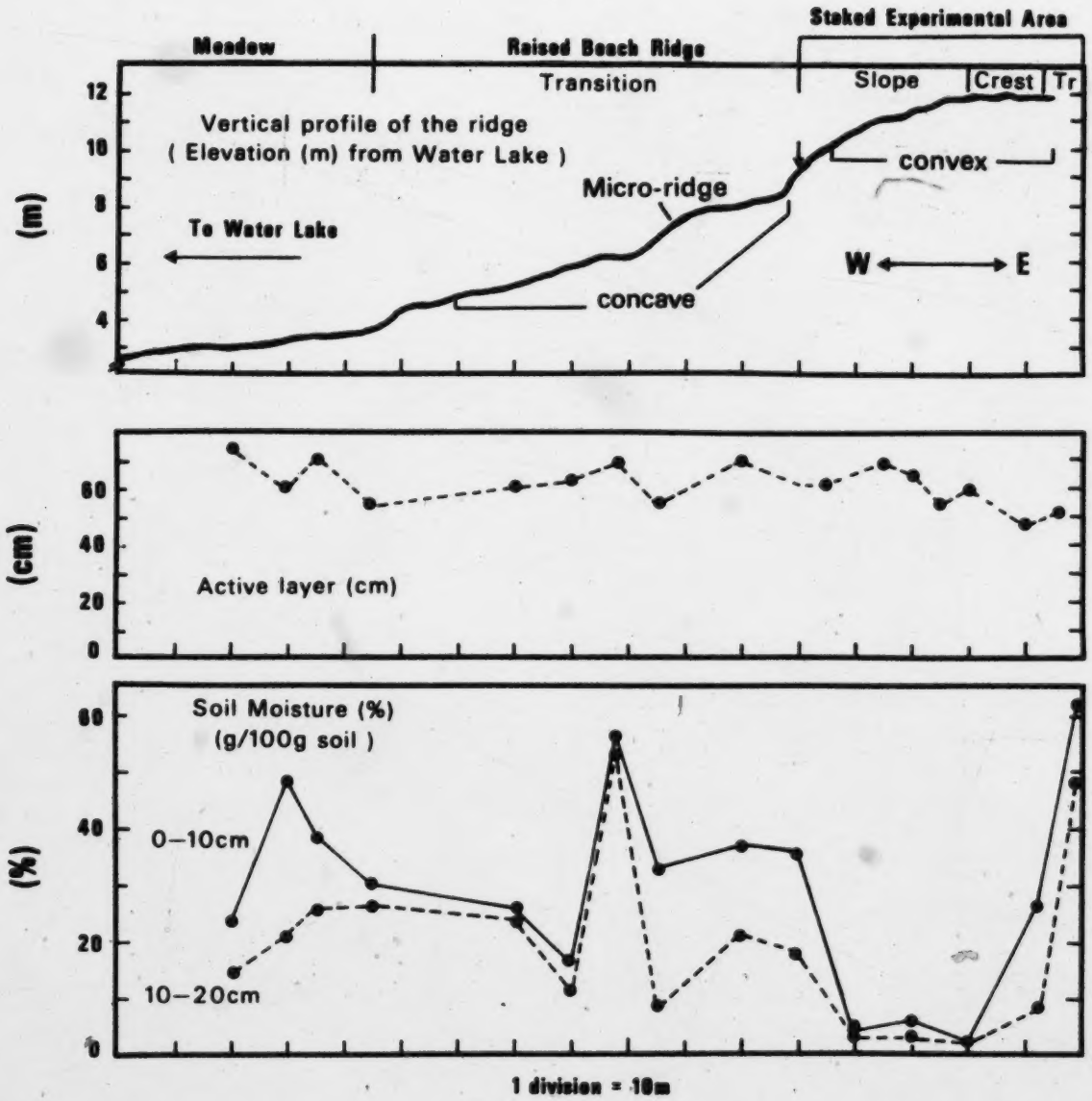

Figure 15. Topographical profile, active layer and soil moisture in the transect across the Intensive Raised Beach (August 13, 1970).

Tolmachev (1966), Khodachek (1969) and many others described the high arctic circumpolar vegetation and collected much information on climate, soils, phenology and plant growth.

Polunin (1951), Bryson (1966), Hare (1970), and Aleksandrova (1970a, 1971) subdivided the circumpolar regions into zones according to various geographic, climatic and other criteria.

Acock (1940) described the vegetation on raised beach terraces in Spitsbergen (78°40'N). He found that the vegetation on older terraces with more mature soils was "more closed" than that on more recently elevated ones. He stressed, however, that other factors such as soil moisture and exposure were more important. These factors graded upon open vegetation on terraces into zones by exposure and moisture, snow cover and relief. Plant invasion and colonization were extremely slow, with only rudimentary succession.

Savile (1972) showed that the total number of species of vascular plants is more closely correlated to July mean temperatures than directly to latitude. Resolute (74°41'N) with its 4.3°C mean July temperature has 70 species of vascular plants, while on Central Peary Land (81° 49'N) 6.4°C mean July temperature was measured and 106 species found. Direct correlation can be seen between number of species and plant size, and consequently is assumed to occur for standing crop and plant production.

Close to the placoric concept* of vegetation (Lavrenko 1968) is Beschel (1969, 1970) who, on Axel Heiberg Island (80°N), distinguished the vegetation complexes, and separated them into five altitudinal belts.

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*The term "placor" characterizes upland habitats which are adequately drained and on which zonal soils and zonal plant formations develop (Aleksandrova 1970b).

He also delimited major vegetation zones on Ellesmere, Axel Heiberg and Devon Islands. His concept of Polar Desert was narrower than that of Aleksandrova. Only the coastal parts (except for Devon Island) were marked by Beschel as Polar Deserts while the rest of the area was calssified as *Luzula* steppe, *Dryas*, and *Cassiope* tundras and Polar steppe. Most of the Devon Island upland was described by Beschel as Polar Deserts. Review of the postglacial history of the arctic vegetation and a new arctic landscape classification are presented in Bliss *et al.*, 1973.

Methods

Information about community structure and species distribution was obtained from quadrate sampling. In the extensive survey of 11 lowland beach ridges, 30 (50x50 cm) quadrats, 10 in each zone, were laid out in a stratified random manner. Species presence, percentage cover, frequency, and number of individual plants were recorded. Data from the IRB were obtained by analysis of 60, 1 x 1 m quadrates, collected also in a stratified random manner. Modified prominence values (PV) were calculated according to Beals (1960):

$$PV = \frac{C\sqrt{F}}{10}$$

C = Cover (%)
F = Frequency (%)

Results and Discussions

The Truelove Lowland beach ridges are being classified as Polar Semi-deserts (Svoboda 1972, 1974, Bliss 1974). Their plant communities differ substantially from the meadows. Species participation as well as total cover and biomass change continually from the foot of the beach ridge, which is the most vegetated site, up to the almost barren crest.

This part of the beach ridge is well-drained but exposed to severe winds and apparently represents a threshold type of habitat for vascular plants. Of approximately 93 species of vascular plants growing in the lowland (Barrett and Teeri 1973), only about 15 species can resist the stress conditions of extreme draught, wind and mechanical damage on the crest. An example of the community pattern on the crest is presented in Fig 16.

The cushion plant-lichen community was described as *Nardino-Dryadetum* by Rønning (1965) and Barrett (1972). It covers most of the slopes and often the crests of older beaches. Younger raised beaches (3-5 thousand years old) have usually less weathered coarse gravel on the surface. Some are steeper and better drained. They can develop extreme xeric conditions, soil water potential of Ψ = -30 bars in July are common. On such exposed and dry crests, *Dryas integrifolia* is absent.

The zone which covers the foot of the raised beach is usually the widest, most mesic part and ecologically appears to be a transition between the cushion plant-lichen community and the frost-boil sedge meadow (Muc 1974a). Its plant community is, however, quite distinct from both communities in the neighbourhood. The similarity with the mesic meadow is in the increasing community cover (between 50-100%), microenvironmental factors such as moisture, and in the increasing portion of sedges. *Carex nardina* is totally replaced by *C. misandra* and this is accompanied by *C. rupestris, C. subspathacea* and sometimes *C. stans*. There is also much *Cassiope tetragona* present. Nevertheless plant cover and biomass vary widely even within zones, microtopography being the most responsible factor.

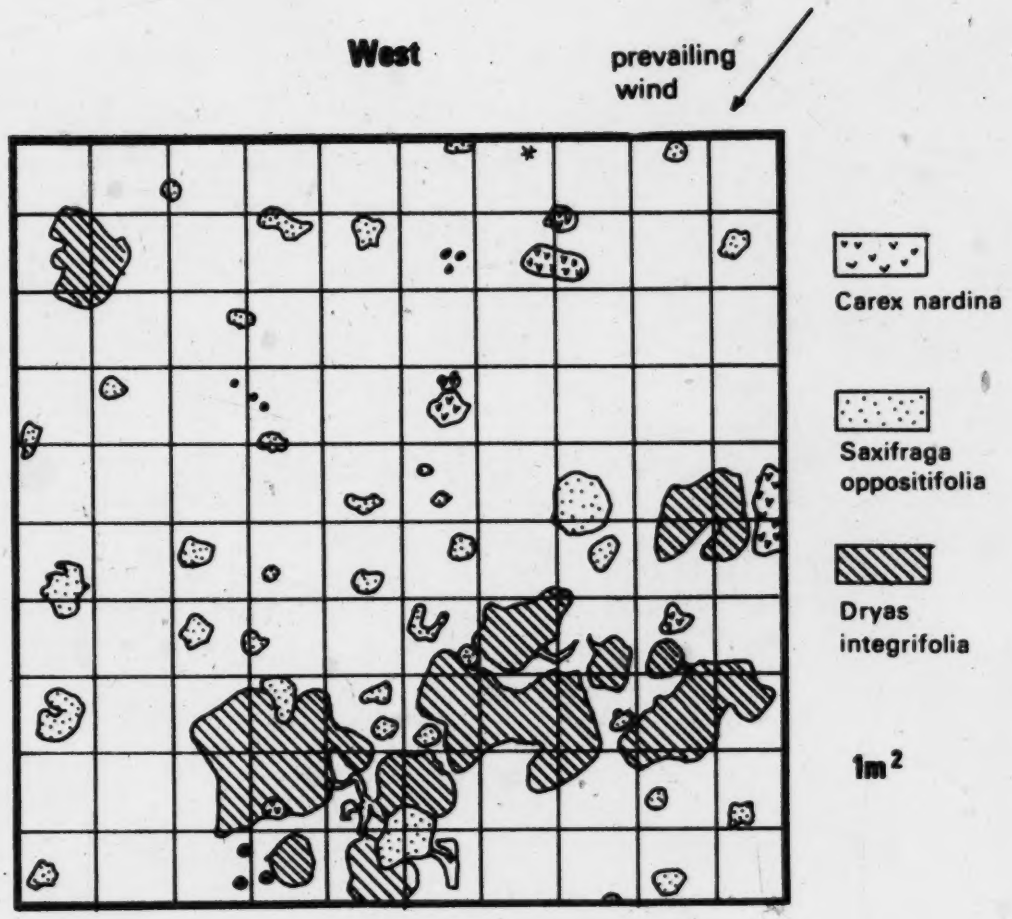


Figure 16. Sample of the Crest Zone community (1970).

Since three physical zones can be recognized, each zone was sampled for plant community composition.

1. The Crest Zone: practically barren with only 10-15% total plant cover. *Saxifraga oppositifolia, Carex nardina* and *Salix arctica* are the main species present. On the crest of IRB, *D. integrifolia* is also important (Table 4). Lichens are mostly crustose; there is very little moss present (Table 5).

2. The Slope Zone: *Dryas integrifolia, S. oppositifolia, Salix arctica* predominate and *C. nardina* alternates with *C. misandra*. Total plant cover averages 25-50% and foliose and fruticose lichens (*Thamnolia vermicularis*) are more abundant (Table 4 and 5).

3. The Transition Zone: the most vegetated zone with total plant cover over 50%. Dominant species are *C. misandra, D. integrifolia, S. oppositifolia, S. arctica* and *Cassiope tetragona*. There are fewer lichens and more mosses (Table 4 and 5).

Other vascular species on the IRB include: *Alopecurus alpinus, Arenaria rubella, Carex rupestris, Cerastium alpinum, Draba alpina, D. bellii, D. subcapitata, Luzula confusa, L. nivalis, Oxyria digyna, Papaver radicatum, Pedicularis hirsuta, P. lanata, Polygonum viviparum, Saxifraga tricuspidata, Silene acaulis, Tofieldia coccinea*. Not all these species are present on every raised beach. Their actual contribution to the total community cover and biomass usually accounts for less than 1%. Low shrub species share more than 50% of the cover in all three zones while all herbs (except for *S. oppositifolia*) contribute less than 1%. Table 5 presents the most common moss and lichen species.

Although there is a continual decline in composition and cover going from the transition up to the crest, the zones can be distinctly

Table 4. Vascular plant cover (%) and number of individual plants (clumps) per m^2 (±St. Error) on the Intensive Raised Beach Site (IRB) in Truelove Lowland (n=60).

	Species	CREST %	CREST No	SLOPE %	SLOPE No	TRANSITION %	TRANSITION No
Woody	*Dryas integrifolia*	7.55±1.3	5.75±0.8	18.68±1.8	12.68±1.9	27.80±1.7	25.40±2.5
	Cassiope tetragona					7.60±3.2	7.07±2.4
	Salix arctica	2.17±0.5	1.80±0.3	0.86±0.2	1.36±0.3	1.88±0.6	2.06±0.6
	Subtotal for shrubs	9.72	7.55	19.54	14.04	37.28	34.53
Monocots	*Carex nardina*	5.80±0.6	14.35±1.5	3.96±0.5	9.52±1.2	0.20±0.0	0.20±0.0
	Carex misandra			0.48±0.2	2.60±1.4	2.08±0.6	11.70±3.7
	Carex rupestris			4.52±1.8	13.76±4.6	13.00±2.8	52.53±7.1
	Subtotal for sedges	5.80	14.35	8.96	25.88	15.28	64.43
Forbs	*S. oppositifolia*	4.05±0.3	37.60±2.9	6.28±0.3	51.00±3.7	4.60±0.6	28.00±5.2
	Silene acaulis			0.05±0.0	0.66±0.0	0.20±0.0	0.66±0.0
	Arenaria rubella	0.04±0.0	1.20±0.4	0.03±0.0	2.48±0.8		
	Cerastium alpinum	0.06±0.0	0.70±0.3	0.01±0.0	0.16±0.0		
	Draba sp.			0.02±0.0	1.32±0.5	0.00±0.0	0.06±0.0
	Melandrium affine	0.00±0.0	0.20±0.0	0.00±0.0	0.13±0.0	0.06±0.0	0.26±0.0
	Ozyria digyna					0.00±0.0	0.40±0.0
	Papaver radicatum					0.00±0.0	0.13±0.0
	Pedicularis lanata	0.05±0.0	0.10±0.0	0.06±0.0	0.40±0.1	0.22±0.0	0.60±0.0
	Polygonum viviparum	0.00±0.0	0.05±0.0	0.00±0.0	0.13±0.0	0.66±0.0	1.60±0.0
	Subtotal for herbs	4.20	39.85	6.45	56.28	5.74	31.71
	Total for community	19.72±1.5	61.75±3.4	34.95±3.0	96.20±6.2	58.30±4.2	130.60±8.4

Table 5. Percentage frequency of main moss species, and percentage cover of main lichen species on IRB (Mosses compiled after Pakarinen*, lichens after Finigan*).

Moss species	Crest and Slope	Transition
Distichium capillaceum	80	90
Encalypta rhaptocarpa	60	40
Mnium riparium	50	80
Bryum sp.	50	20
Myurella julacea	40	40
Isopterygium pulchellum	20	20
Dicranoweisia crispula	20	
Didymodon asperifolius	20	
Myurella tenerrima	20	
Ditrichum flexicaule		70
Tomenthypnum nitens		40
Drepanocladus intermedius		30
Blepharostoma trichophyllum		30
Aulacomnium turgidum		30
Hylocomium splendens		30
Pogonatum alpinum		20
Drepanocladus uncinatus		20
Orthothecium chryseum		20
Timmia norvegica		20

Lichen species	Crest	Slopes	Transition
Crustose			
Rhizocarpon geographicum	3.3	1.9	
Lecanora dispersa	1.0	1.2	
Lecanora epibrion	3.4	18.0	1.5
Foliose			
Umbilicaria arctica	4.4		
Umbilicaria lyngei	1.2		
Parmelia separata	0.6		
Hypogymnia subfusca	1.7		
Physcia muscigena			1.9
Fructicose			
Cetraria aculata		0.5	3.6
Cetraria islandica		1.0	
Cetraria nivalis	0.5	1.7	0.5
Alectoria chalybeiformis	0.6		
Alectoria nigricans	2.2	1.2	
Alectoria ochroleuca	2.9	0.9	
Alectoria pubescens	11.4		
Thamnolia vermicularis	4.4	6.7	5.5

Moss species with frequency values less than 20% and lichens with cover values less than 0.5% are not included. (Freqnency values are based on 40 cm^2 sample plots).

*personal communication. For detailed information see Pakarinen and Vitt (1973) and Richardson and Finegan (1973)

recognized and the sampling technique developed.

Analyses of the Extensive Study data show that there is a correlation between plant cover, biomass, and age and elevation of the raised beaches, as was already pointed out by Acock (1940) on Spitsbergen. Location of sampled raised beaches can be found on Fig. 1.

The differences are most pronounced in the Crest and Transition Zones. Relatively young raised beaches (3000-5000 years) have less cover and biomass than those 6000-8000 years old (Fig. 17). This suggests that there has been a certain pattern in revegetation of the entire lowland area where beach ridge age and elevation, stage of weathering of the ground surface rocks, distance from the coast, and probably some other factors are involved.

Plateau: On the plateau, vascular plant cover is very low (<10%) and total vascular plant biomass ranges from 0-70 gm^{-2}. Plants, if present, grow mainly between rocks exposing only minimal area above the surface. Figure 18 shows the undisturbed fellfield without any apparent plant life. A detailed photograph of the ground surface (Fig. 19a) shows some plants protruding between the rocks but not overtopping the rock surface. When the surface rocks were removed plant life became surprisingly apparent (Fig. 19b). Most of the plant biomass is formed by moss, however, there are some vascular plants. The Moss/Vascular Plant standing crop ratio = 11.2. The ratios calculated from 1970 data include: Shoot/Root = 3.47; Live/Dead = 1.06. The list of vascular species from the Plateau and their cover values are presented in Table 8.

Discussion

In the botanical literature, Polar Desert is a well established

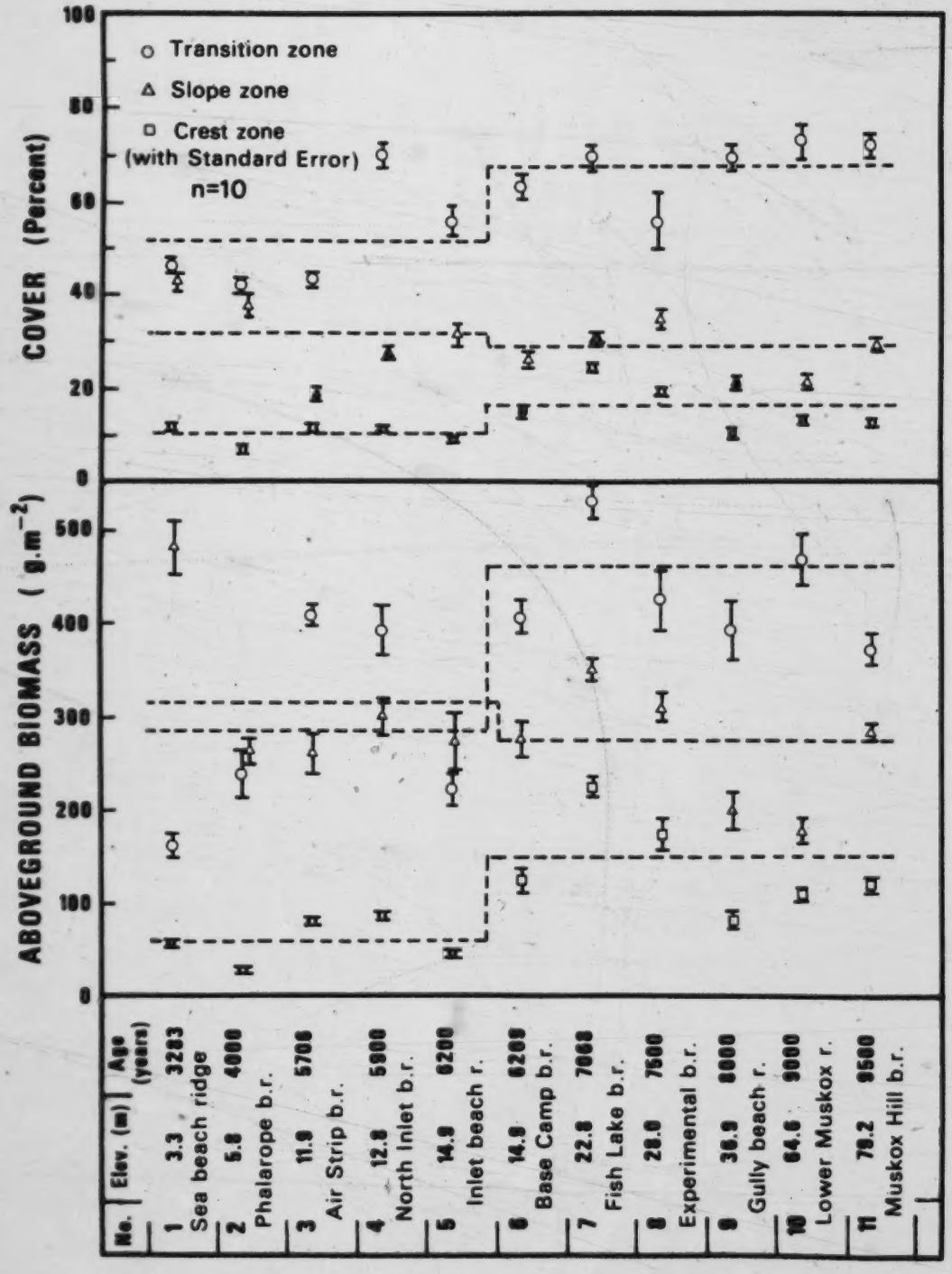

Transition zone
Slope zone
Crest zone
(with Standard Error)
n=10
COVER (Percent)
ABOVEGROUND BIOMASS (g.m⁻²)
No. | Elev. (m) | Age (years)
1 3.3 3283 Sea beach ridge
2 5.8 4000 Phalarope b.r.
3 11.9 5700 Air Strip b.r.
4 12.8 5900 North Inlet b.r.
5 14.9 6200 Inlet beach r.
6 14.9 6200 Base Camp b.r.
7 22.8 7000 Fish Lake b.r.
8 28.0 7500 Experimental b.r.
9 36.9 8000 Gully beach r.
10 64.6 9000 Lower Muskox r.
11 78.2 9500 Muskox Hill b.r.

Figure 17. Community cover and aboveground standing crop on raised beaches, Truelove Lowland (1971). The dashed lines represent a mean of the particular group of points, (n=10).

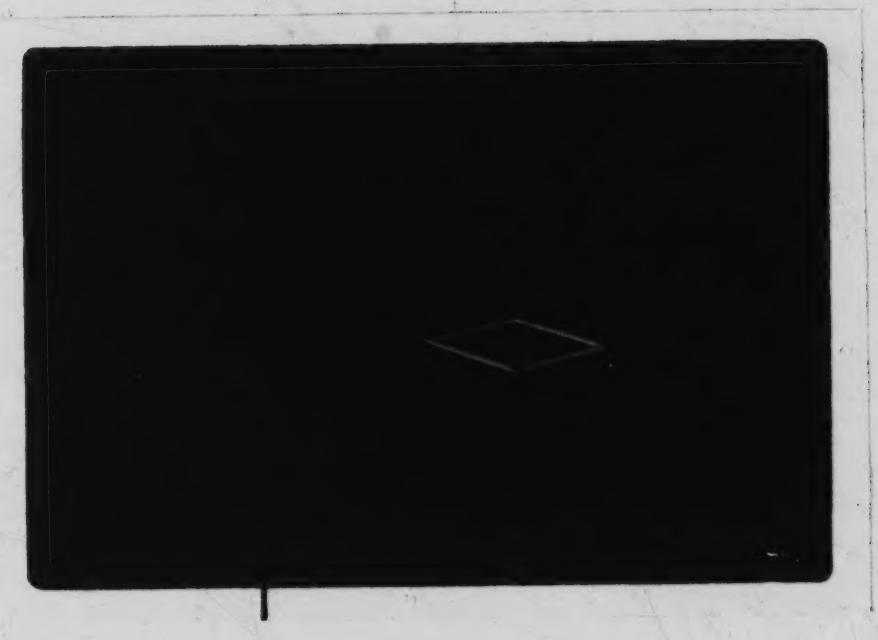


Figure 18. Fellfield plain with sorted polygons on the East Plateau.

a.

b.

Figure 19. Plant life hidden between and under rocks (a) and plant biomass' relative abundance when the surface rocks are removed (b).

concept documented in works of Anderson (1935), Gorodkov (1943, 1949, 1958), Bocher (1949), Fredskild (1961) and others. Aleksandrova (1970b, 1971) reviewed the classification of the Arctic by twenty Russian authors.

Aleksandrova's system (1970b) was based on ecological and phytocenological rather than on merely geographic or strictly climatic criteria. She adopted Lavrenko's (1968) system of placoric habitats where the bases for the zonal partition was floristic composition, characteristic life forms, and structure of placoric communities on loam soils. Aleksandrova recognized two main arctic zones: Polar Desert with the North and South Polar belts, and Tundra divided into Arctic Tundra subzone (with North and South belts) and Subarctic Tundra subzone (with North, Middle and South belts).

It is obvious that detailed delimitation of zones using these ecologic criteria will result in a mosaic of areas without smooth, latitudinally oriented division lines, and with even higher intermingling on a subzonal and belt level. It will, however, reflect the true situation and natural position of Polar Desert and Tundra habitats and their sub-categories.

The Devon Island upland fulfills the specifications of a true Polar Desert, designated by Aleksandrova (1970b). During the growing period the mean temperature is close to 0°C. The vegetation is strictly Arctic in composition, discontinuous in cover with a high percentage of barren ground, restricted in vertical structure and with a poorly developed root system. Apomyxis prevails over the reproduction by seeds because most of the polar desert plants remain sterile, though they bloom. Mosses and lichens represent an additional stress factor for the

flowering plants, because they grow in clumps, they utilize moisture and nutrients that would otherwise be available to the vascular plants. In addition, tight clumps of lichens may physically shade and mechanically prevent growth of the flowering plants.

Polar Desert soils are very poorly or not at all developed, they are neutral or alkaline with high base saturation and with irregular accumulation of humus in isolated pockets, usually under growing plants.

The Tundra zone on the other hand has a mean July temperature lower than +10°C, but higher than 0°C. An abundance of herbaceous perennials and dwarf shrubs form dense polydominant communities with only spots of bare ground. Hummocks are common. Characteristic is a genetic non-homogeneity of floral elements as a result of species migration. At the northern edge of the arctic tundra denuded polygonal tundra covers large areas. Prostrate shrubs occur only as a local admixture in an herb layer. The automorphic soils, namely the Arctic Brown, are relatively well-developed but minor in extent. However, they represent the only zonal soil on the lowland.

In this study information about plant distribution, its structure and biomass within the true Polar Desert represents an important comparative check for the Polar semi-desert vegetation on raised beach ridges.

This study has been mainly concerned with biomass distribution and production of vascular species on raised beach ridges, regardless of the fact that phytocenologically these data may be derived from different plant associations. The agreement to treat raised beach ridges as a vegetational and ecological unit was dictated by the overall project design, which recognized three major types of plant community -

landscape units in the lowland: sedge dominated meadows, cushion plants on raised beaches, and dwarf heath shrubs in rock outcrops.

Only basic information about plant cover and species composition are being used in this chapter. Further data are tabulated together with information about standing crop in the Production chapter and are also included in the Appendix.

Phenology and Plant Growth

Methods

Periodic observations and measurements on labeled vascular plants were concentrated on the IRB. In 1970 and 1971 general observations were made of breaking of dormancy and flowering of most of the species. In 1972 detailed observations were made on 100 plants each of *Dryas integrifolia* and *Saxifraga oppositifolia* (50 individuals of each species in the Crest and Transition Zone). The Slope Zone was not sampled because of time. Three phenological stages: flower bud formation, full flower, and post-flowering were recorded throughout the entire growing season.

The clump area of all labeled and observed plants was measured and flowering was correlated with clump size and in this way with relative clump age. Simultaneously, species distribution was compared in the two zones. Photographs of the crest and transitional "ecoforms" of each species were taken for documentation. Standing crop per plant area was calculated for each zone using the data obtained by harvesting from 5 additional raised beaches in 1971 (5 samples 5x5 dm per zone per beach ridge).

Because of the difficulty in measuring growth of tiny leaves and shoots of these high arctic cushion plants, an indirect technique was chosen in order to obtain information about plant growth. In 1971 and 1972 shoots of several species were regularly collected. Some shoots were pressed as herbarium specimens and others preserved in a formalin-acetic acid-alcohol fixative. Later, the collected material was analysed and individual preserved shoots and roots measured.

Results and Discussion

Phenology

Immediately after snowmelt, soils were water saturated. Plants on the crests and slopes take advantage of this and develop rapidly. The water drained quickly and the crest dried.

The transition (snowbed) community began growth 2-3 weeks after the crest community. This results in a different plant composition, cover and strategy in these zones as in similar situations mentioned by Jashina (1961), Billings and Mooney (1968), Bliss (1971) and Teeri (1972).

Saxifraga oppositifolia is usually the first to flower, usually 305 days after snowmelt. In *Saxifraga oppositifolia* a -2°C plant temperature is sufficient to break dormancy and 0°C to stimulate flowering in plants grown in a plant growth chamber. Species such as *Dryas integrifolia, Salix arctica, Cassiope tetragona, Pedicularis lanata,* and *Silene acaulis* begin to flower 5-20 days later. The latest species to flower are *Carex nardina* and *C. misandra* (Table 6).

Phenological events of *D. integrifolia* and *S. oppositifolia* as well as other species growing on the Crest and Transition Zone differ by more than two weeks, being controlled by snowmelt patterns. In the

Table 6. Phenology of the dominant species on the Intensive Raised Beach Site, Truelove Lowland (1971).

Zone	Species	Growing season on the Exp. raised beach ridge in weeks.								
		13 - 19 June	20 - 26 June	27.June -July 3.	4 - 10 July	11 - 17 July	18 - 24 July	25 - 31 July	1 - 7 August	8 - 14 August
Crest	Saxifraga oppositi-	snow	part.free of snow some flo-ers	flowering	flowering	seed for-mation	seed ripening	seed ripening	mature seed	new flo-wer bud initiation
slope	Salix	snow	free of snow, dor-mant shoots	leaf buds opening	leaf de-velopment sporadic flowers	leaf growth, full flowers	leaf growth, some flowers	Seed formation & ripe-ning	some lea-ves yellow seed ripening	Many lea-ves yel-low,seed mature
slope	Pedicularis lanata	snow	gray, dead shoots only	new shoot initiat	sporadic flowers	full flowering	flowering	Some flowers seed formation	seed formation & ripening	seed ripen-ing
slope	Dryas integri-folia	snow	brown clumps	brown-red tips	red-green tips	green leaves	flower initiation full flower-ing	flowering seed formation	seed formation & seed ripening	mature seed, leaf red-dening
transition	Cassiope tetragona	snow	snow	brown-green tips	greening tips	some flowers	flowering	flowering	some flowers seed formation	seed forma-tion
slope	Silene acaulis	snow	gray clumps	greening clumps	New leaf full growth	some flowers	full flowering	flowering	some flowers	seed forma-tion
crest	Carex nardina	snow	brown clumps	green leaf bases elongate	leaf elongation	inflorescent formation	some flowering	full flowering, leaf die back	seed formation leaf die back	seed ripening intens. leaf die back
Transition	Carex misandra	snow	part.free of snow	greening clumps	leaf growth	inflores-cence formation	flowering	flowering	some flowers	seed formation & ripen

late and cool summer of 1972 many *Dryas* flowers growing in the Transition Zone froze while in full bloom in late August while the previous two years flowering was over by the end of July.

The same phenological pattern occured in plants growing on "early" or "late" melting raised beaches. For example on July 20, 1972 when the crest of IRB (elev. 28 m) had the first spots of snow-free ground, the crest of the Base Camp (#6) raised beach (elev. 14.9 m) was 5-15% free of snow with approximately 5% of the total *S. oppositifolia* in flower initiation and 30% of plants in full flower. About 80% of the exposed *Salix* plants were in flower here at the same time.

Figures 20 and 21 give detailed information on phenology of *Dryas* and *Saxifraga* on the IRB. Clumps of both species show a similar phenological pattern in all size classes of the same zone. However, the curves differ in shape between zones. In the transition, flowering of *Dryas* is distributed over a longer period of time and its flowering stages widely overlap. *Saxifraga oppositifolia* sets flowers more abruptly in the transition and the period of flowering is significantly longer compared with flowering on the crest.

Plant size and zonal distribution

Although *D. integrifolia* and *S. oppositifolia* are two major components of this cushion plant-lichen community, both species have significantly different microhabitat requirements. While both species have a relatively wide tolerance to soil moisture regimes, the optimal site for *Dryas* is the mesic Transition Zone while *S. oppositifolia* flourishes with little competition from other vascular plants in the xeric Crest Zone. Photographs of the morphological variation between

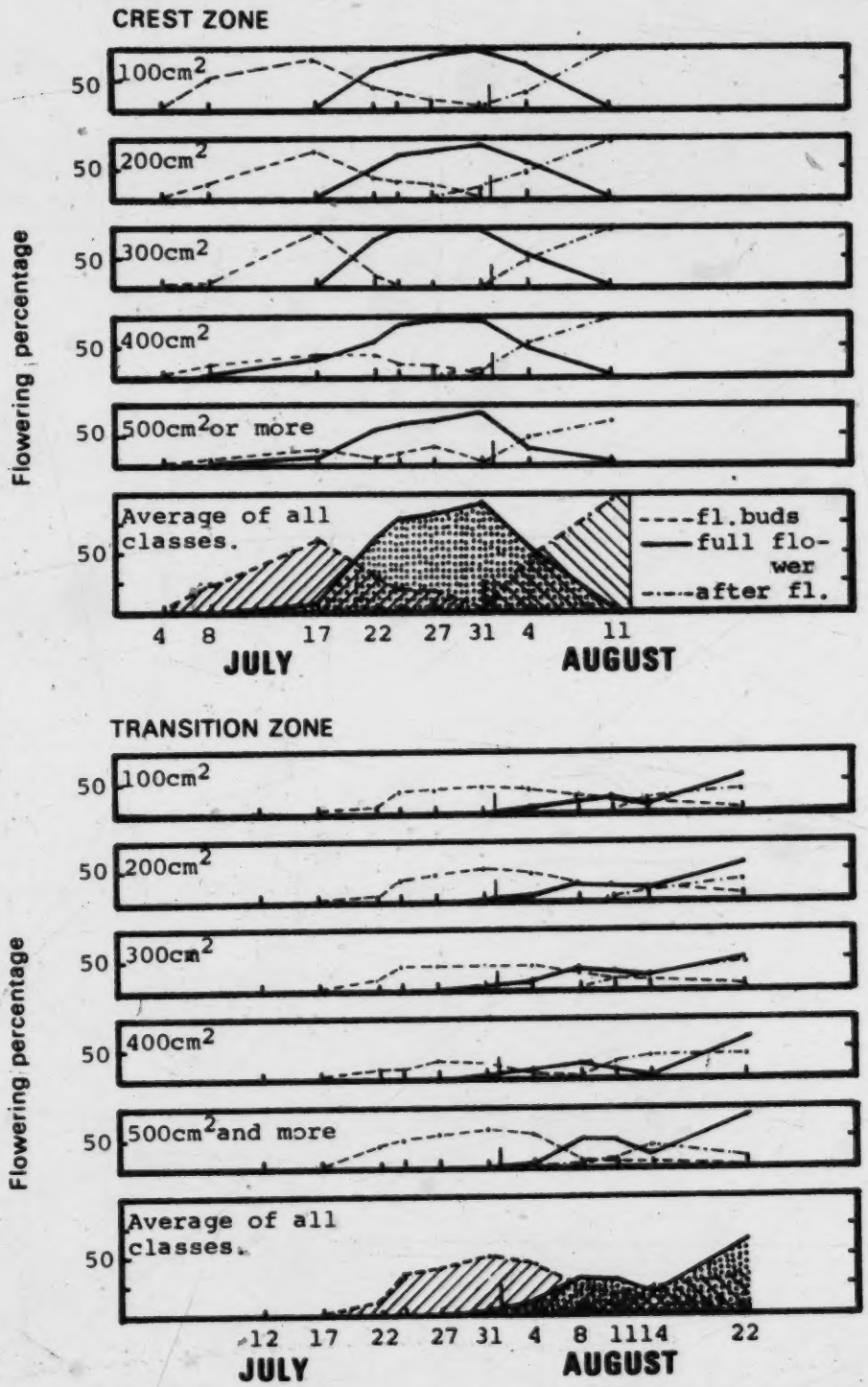


Figure 20. Pattern of flowering in different size classes of *Dryas integrifolia* clumps expressed as percentage of total flowering. IRB 1972.

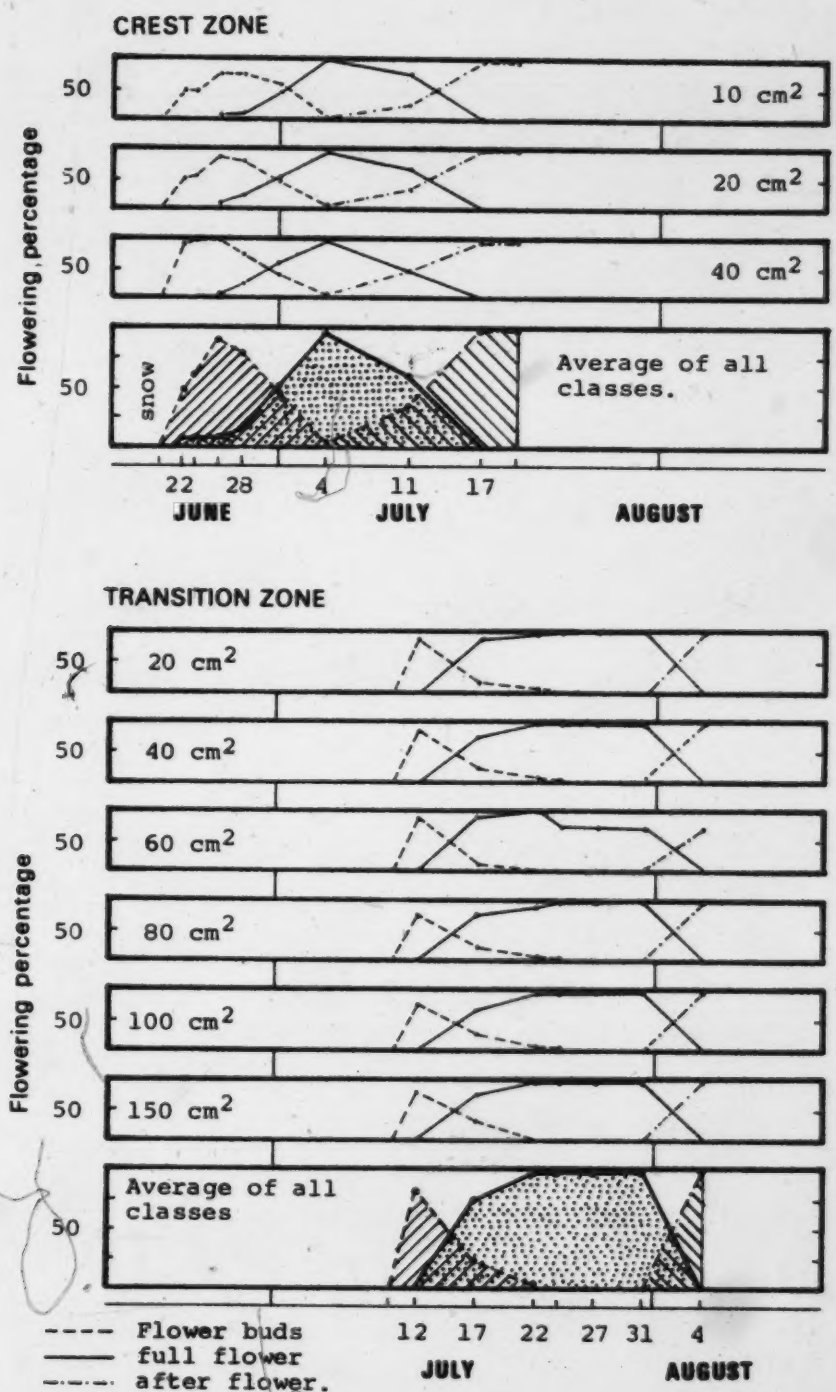


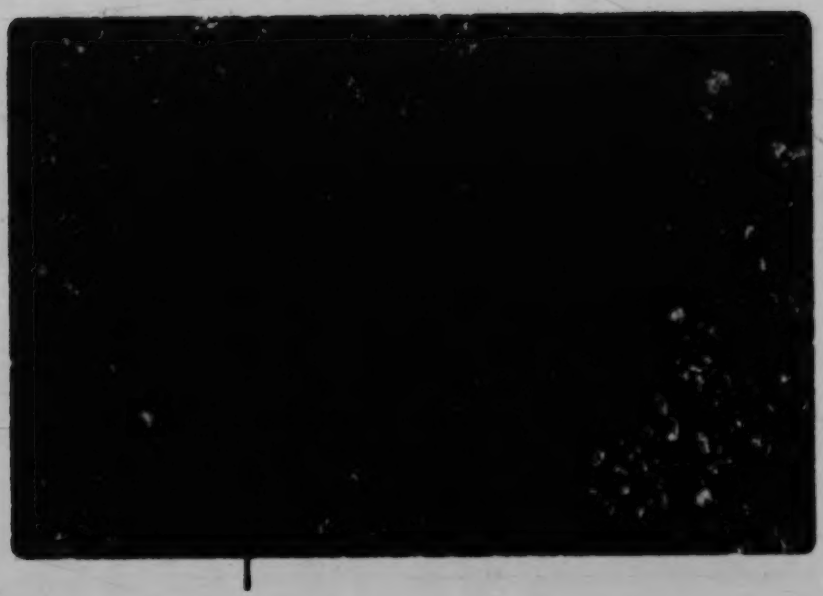
Figure 21. Pattern of flowering in different size classes of *Saxifraga oppositifolia* clumps expressed as percentage of total flowering. IRB 1972.

the typical crest and transitional ecoforms of both species are presented in Figures 22 and 23.

On some crests, *Dryas* plants can hardly survive beside the two better adapted species *Saxifraga oppositifolia* and *Carex nardina*. At the driest sites *D. integrifolia* is completely absent, a fact that encouraged Barrett (1972) to describe this extremely xerophytic plant community as the *Nardino-Alectorietum* association. Where dwarf mats of *Dryas* plants are present, they are flat and prostrate, the most frequent clump size being 100 cm^2. Most of the plant surface is dead. On the contrary, *Dryas* clumps growing in the mesic Transition Zone are hemispherical, with most of the cushion surface being green and producing more flowers. The most frequent clump size falls into the 200 cm^2 class (Fig. 24). This explains why in the transition the average number of flowers increases with the clump size almost linearly and why the clumps are generally larger. Figure 24 also demonstrates the size distribution of *D. integrifolia* clumps in both zones and average number of flowers per clump as well as some other parameters. Figure 25 presents the same information for *S. oppositifolia*.

Both *Saxifraga* and *Dryas* clumps decrease in size with the higher position on the ridge. Both species, however, differ in flowering pattern and other parameters. On crest, *Saxifraga* forms compact cushions with more shoots and flowers per plant unit area while in the transition more lossely creeping and fewer flowers are found. On the other hand, on crests *Dryas* clumps are always partially dead with less biomass and fewer flowers. Consequently the *Saxifraga* standing crop shows a high correlation with cover in the Crest and Slope Zone but a much lower correlation in the Transition Zone (Fig. 26).

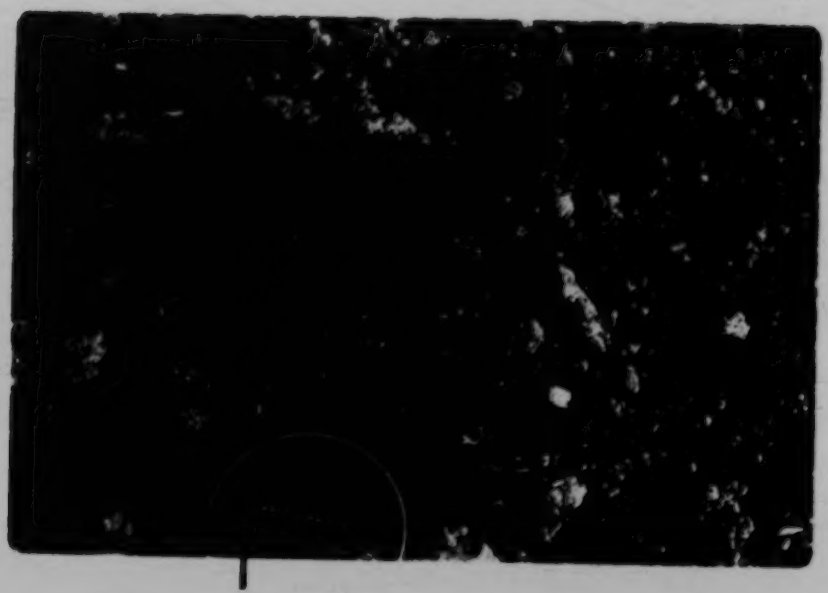
a.



b.

Figure 22. Ecoforms of *Dryas integrifolia* growing in Crest (a) and Transition Zone (b).

a.



b.

Figure 23. Ecoforms of *Saxifraga oppositifolia* growing in Crest (a) and Transition Zone (b).

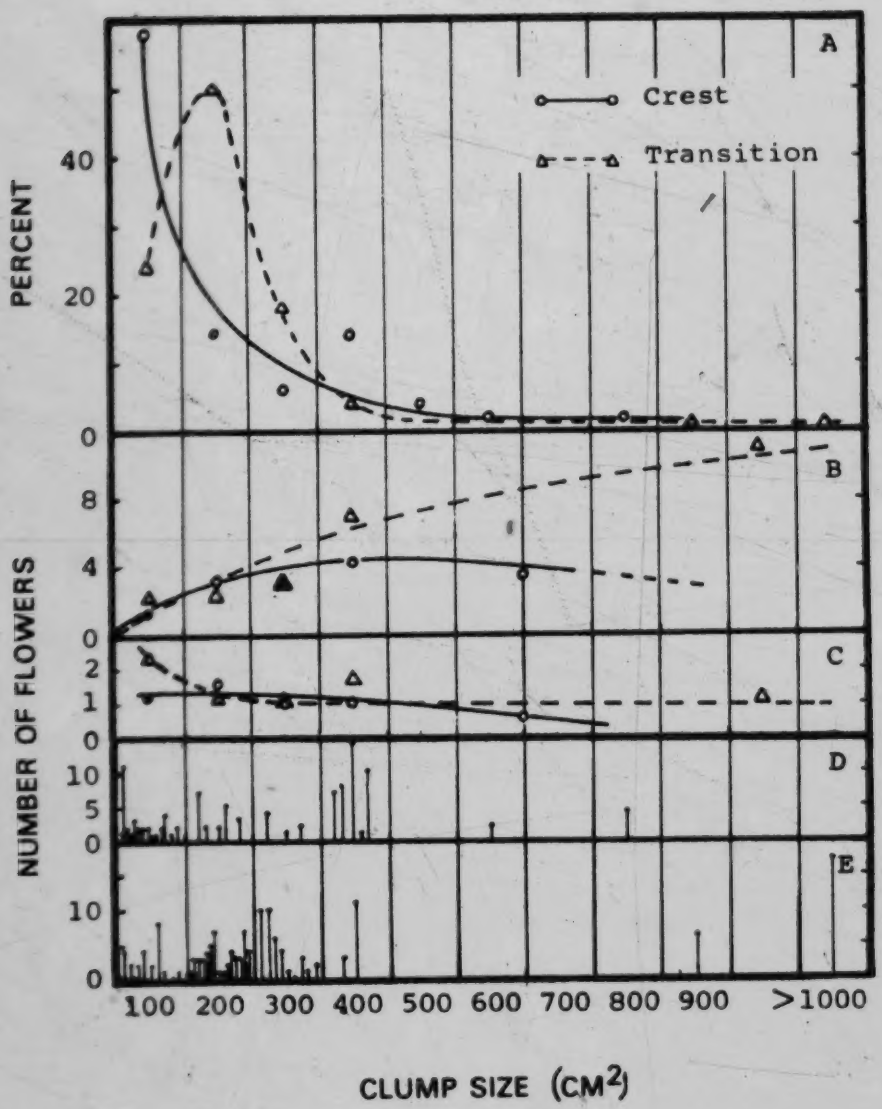


Figure 24. Size distribution of *Dryas integrifolia* clumps in the Crest and Transition Zone (A), average number of flowers per clump in the different size classes (B), average number of flowers per 100 cm^2 in each class (C), actual variation of flower numbers per clump in relation to clump size in the Crest (D) and in the Transition Zone (E).

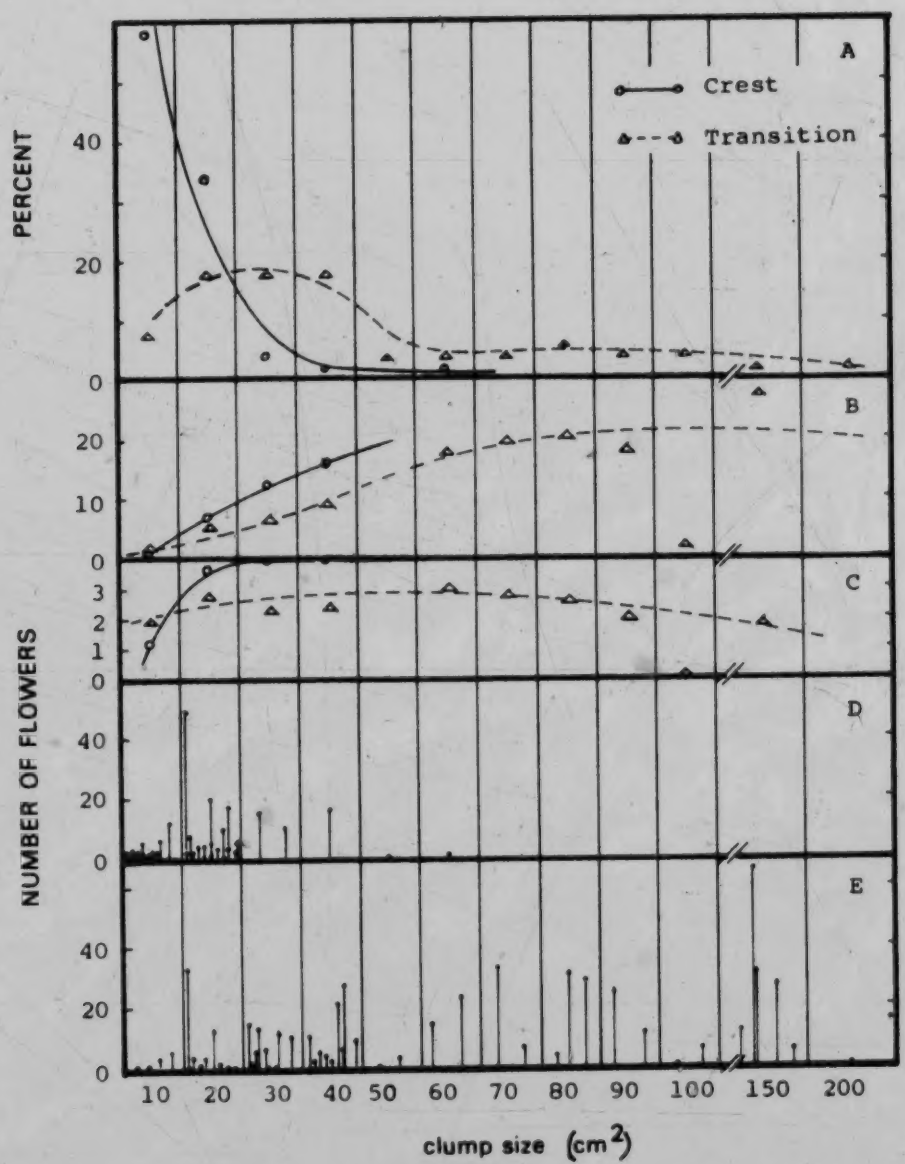


Figure 25. Size distribution of *Saxifraga oppositifolia* clumps in the Crest and Transition Zone (A), average number of flowers per clump in different size classes (B), average number of flowers per 10 cm^2 in each class (C), actual variation of flower numbers per clump in relation to clump size in the Crest (D), and in the Transition Zone (E).

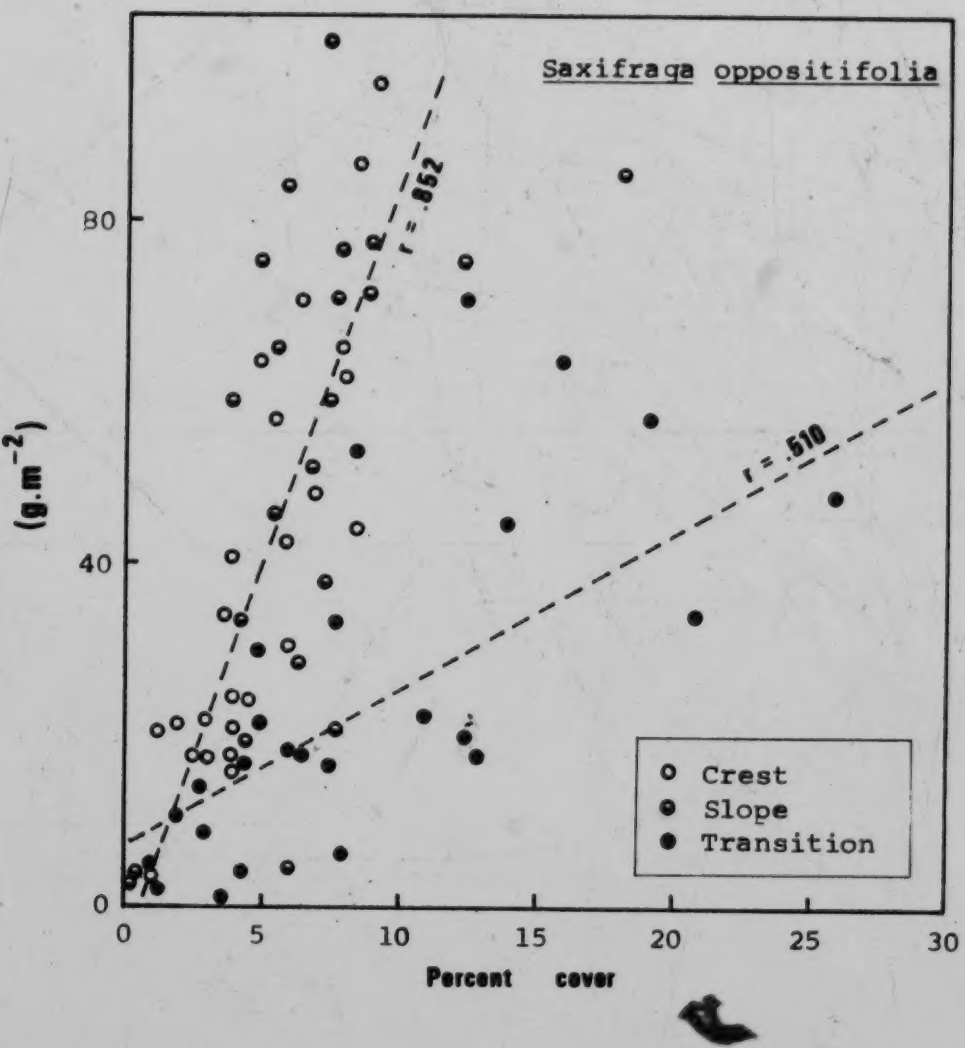


Figure 26. Aboveground standing crop of *Saxifraga oppositifolia* in relation to plant cover in different beach ridge zones. (The correl. coef. is significant at the 5% level).

This illustrates why *Saxifraga oppositifolia* is a common member of polar desert plant communities. *Dryas* prefers the dry mesic sites and cannot be therefore classified as a purely xeric species. *Dryas* is missing in a true Polar Desert, or on a limited scale occurs only in protected habitats. *Saxifraga oppositifolia* completes its flowering shortly after snowmelt while water is still available. *Dryas* needs a longer period of sufficient moisture to complete the flowering.

This cannot be proved simply by comparison of cover and standing crop values between these two species within one isolated zone. *Dryas* if present, always shows higher figures than *Saxifraga* because it forms larger cushions. When examined more closely the independent pattern of distribution of the two species is more clearly shown.

Plant growth

There is very little annual growth in arctic cushion plants such as *D. integrifolia, S. oppositifolia, Silene acaulis*, etc., in clumped sedges such as *C. nardina, C. misandra,* or in low shrubs such as *Cassiope tetragona* and *Salix arctica.* By direct observation it is difficult to distinguish the previous year's green portion from that of the present year in the evergreen and semi-evergreen species. My observations and those of Savile (1972) are that green leaves of many arctic cushion species last for more than one season. To determine the rate of leaf production per year, shoots of *Dryas* and *Saxifraga* were examined in detail (see Methods, p.50).

Dryas integrifolia: Each shoot of *D. integrifolia* starts the growing season with an average of 2.6 old leaves and has 5 green leaves (on the average) in early August. After snowmelt they are reddish brown but

during the next two weeks new chlorophyll forms and the leaves turn green again. In analysing the 1970 data the author assumed that all brown leaves had perished during winter and that all green leaves were newly formed. This error was revealed by further observations in 1971 and the 1970 data were corrected. Close to the end of the growing season, in mid-August, green leaves turn red again, with the new leaves of that season again turning green the following summer. Figure 27a shows the changes in leaf length in old and new leaves of *D. integrifolia* in the Slope Zone during 1971. *Dryas* is present from top of meadow hummocks up to the most raised beach crests. For more information on *Dryas* growth and ecology see chapter: *Dryas* clump as a microecosystem (p.150).

Saxifraga oppositifolia: Each shoot of *S. oppositifolia* has on the average 7-8 leaves from the previous year and produces another 7-8 leaves during the growing season so that in mid-August there are 14-16 leaves in each rosette. Figure 28 illustrates leaf size and number in *Saxifraga* from five random replicates collected several times during 1971.

In contrast with *Dryas*, leaves of *Saxifraga oppositifolia* do not redden in autumn. The older leaves die back at the end of the season and the plant carries on with a small green rosette of leaves next spring. As with *Dryas*, the dead leaves remain on the shoot for many further years buffering and protecting the internal clump environment against temperature and moisture fluctuations.

Carex nardina: *C. nardina* growth occurs in compact bunches of shoots connected together with very short rhizomes. This results in an age zonation within a clump. Some regions are young and growing more

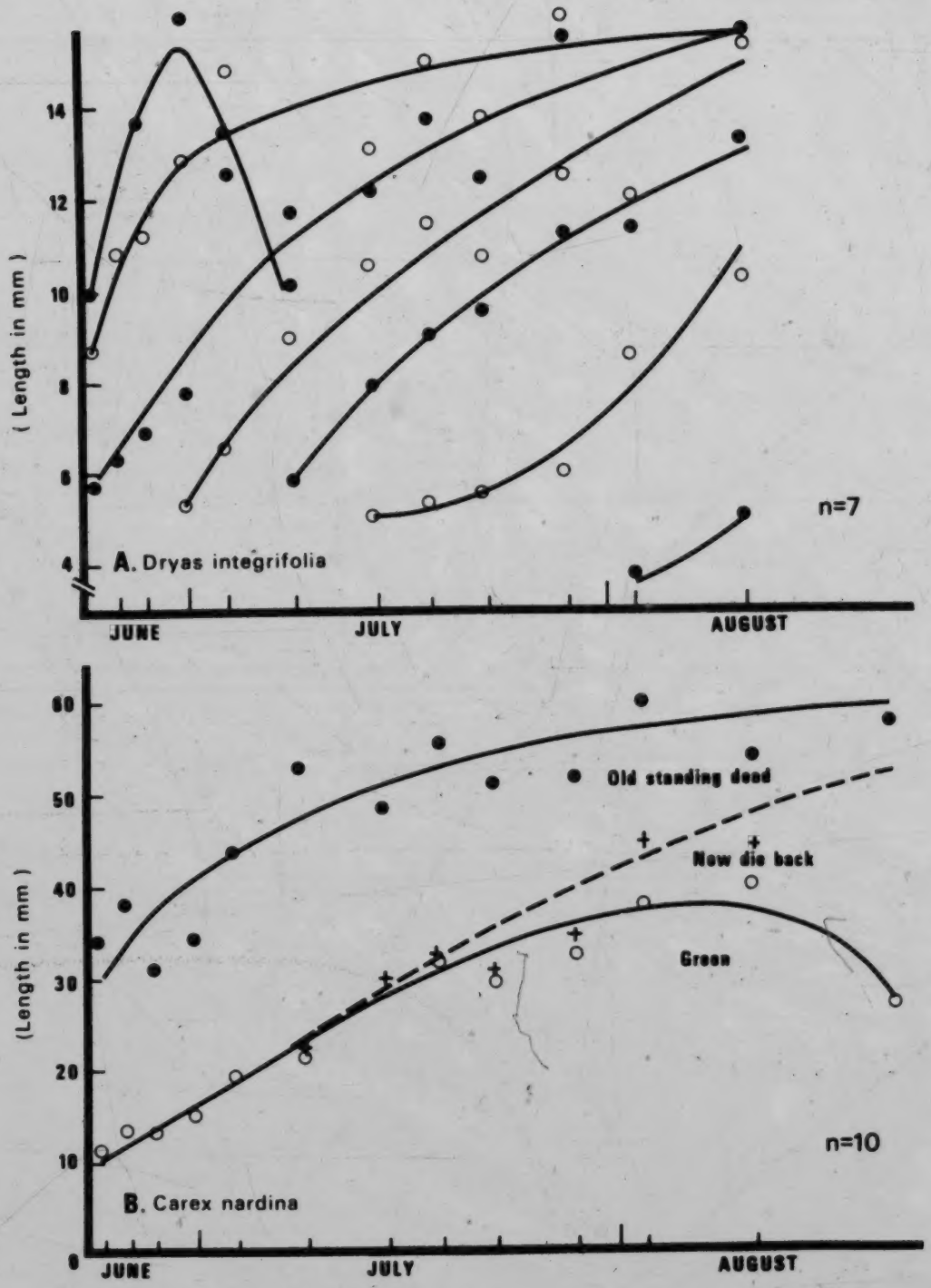


Figure 27. Leaf development as depicted by growth curves (plastochrones) of successive leaves of *Dryas* (A) and *Carex nardina* (B).

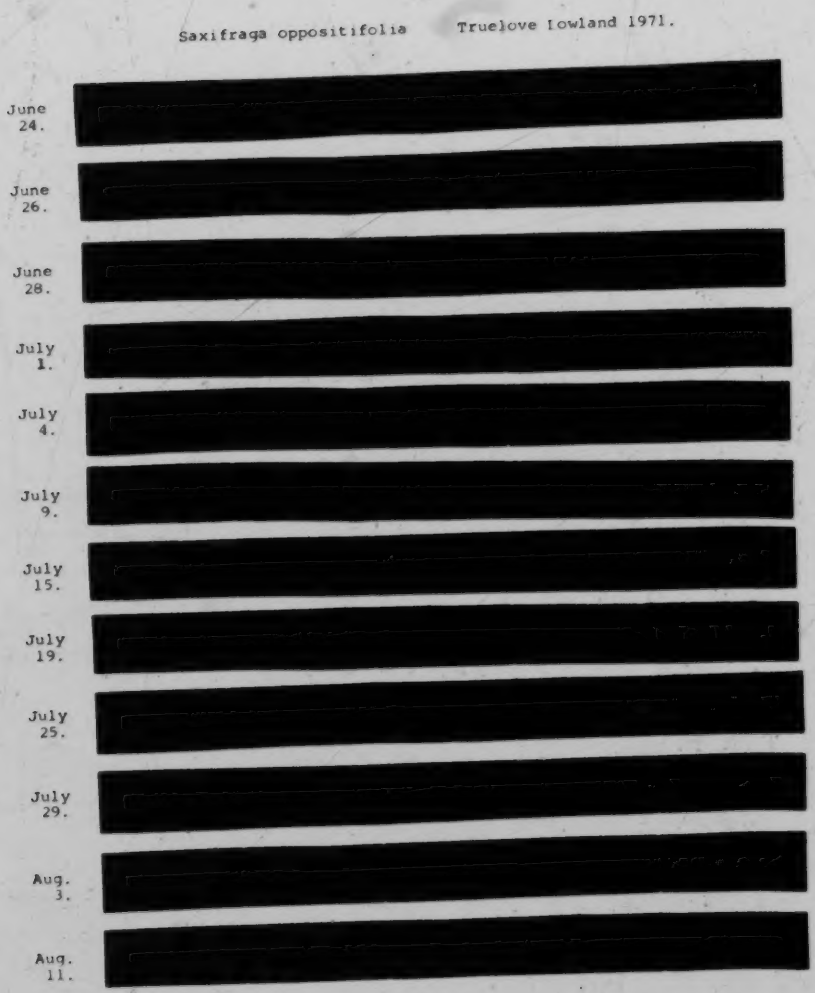


Figure 28. *Saxifraga oppositifolia* development of a leaf rosette on crest, during the season 1971. Five randomly selected replicates out of 20 sampled were analysed on each date. (3/4 of the actual size).

vigorously while others are old and dying. Dead portions of a clump can be easily recognized and separated.

Carex nardina leaves elongate for several years before they are replaced. The actual life time of one individual leaf can be expressed by the formula:

$$A = f \frac{Ns}{Ni}$$

A = Mean age of an individual shoot
Ns = Number of shoots in a clump
Ni = Number of inflorescences in a clump
f = Factor approaching unity if virtually every shoot eventually reaches flowering

The life cycle of a *C. nardina* shoot is completed after flowering. Assuming that almost every shoot will eventually reach the stage of flowering, the life span of an individual shoot can be calculated from the above formula. In this case a single leaf of *C. nardina* would stay alive for many years growing and dying back every year because the number of inflorescences in a clump formed per year is very low.

The actual growth of *C. nardina* leaves is continuous over the entire season as is illustrated in Figure 27b. Leaves carry the previous year's standing dead which breaks off during the growing season and is replaced by new die back from the current season. *C. nardina* grows only on crests and slopes, almost never in transitions or meadows.

Carex misandra: The growth form of *Carex misandra* resembles closely that of *C. nardina*. It occurs on lower slopes and in transitions and also forms dense and compact tufts but the individual shoots have more leaves in distinct bunches attached together with very short rhizomes. Leaves are 3-5 mm wide and follow a similar growth pattern as described in *C. nardina*. Leaves last several years growing and dying back every season.

Salix arctica: There is a marked difference in size and vigor of *Salix arctica* plants according to habitat. The species has one of the widest ranges of tolerance to microclimatic conditions of any arctic species. In the Truelove Lowland it grows from the most xeric sites on crests of raised beaches down to hummock tops in fairly moist meadows, in rock outcrops as well as on slopes of both granitic and sedimentary cliffs, and also on the edge of the plateau above the lowland. Measurements and observations of *Salix* populations were mainly conducted on the slope of the IRB. The data show a high variation in leaf size between individual plants and even between various twigs of the same plant. This supports the idea that this species is highly plastic and sensitive to small changes in environmental conditions. Warren Wilson (1964) discussed the increasing size of *S. arctica* growth rings from the High Arctic to the Subarctic. Similar conclusions can be made about the growth rate of shoots, shrub size, number of leaves per shoot, and leaf size of plants distributed along the transect from the most dry to fairly moist habitats.

Salix arctica in the Truelove Lowland develops 3-6 leaves on each terminal shoot per year. Catkins expand immediately after snowmelt. The leaves, however, start to expand approximately 7-10 days after the snowmelt. They develop relatively slowly, reaching full size in three weeks. At maturity leaf length varied between 17.0-25.2 mm (blade and petiole) and 9.2-11.8 mm in width on the slope. There is a distinct gradation in leaf size from the first to the last leaves produced in a season (Table 7).

Table 7. Mean leaf parameters for *Salix arctica*. Data are expressed in mm ± SE (n = 15).

Leaf sequence from the first to the last	Petiole (mm)	Blade length (mm)	Blade width (mm)
1	3.3 ± .36	15.9 ± .95	7.3 ± .37
2	2.9 ± .33	14.3 ± 1.0	7.4 ± .36
3	2.5 ± .44	12.2 ± 1.3	6.6 ± .70
4	3.3 ± .44	14.4 ± 1.6	7.4 ± .70
5	2.4 ± .28	13.0 ± .97	7.0 ± 1.0

On the slope the average annual shoot elongation of *S. arctica* was found to be 7.7 mm ± .42 (n = 87).

Winter growth

While winter growth has been reported in *Deschampsia flexuosa* in the Murman District of the USSR (Kovakina 1958) and in *Kobresia bellardii* in the alpine tundra of Colorado (Bell 1973) there is no evidence of winter growth in the high arctic species examined by the author and Muc (1974) on Devon Island . All the species appear to be deeply dormant until snowmelt when breaking of dormancy can be rapid as with *Saxifraga oppositifolia* and *Salix arctica*. Winter inactivity is in part a function of the three months of total darkness and the very cold soil temperatures resulting from low permafrost and air temperatures.

Discussion

Phenological observations and remarks on flowering of high arctic plants are sporadically available from the time of the earliest arctic explorers. Systematic data, however, are of much later date. Sørenson (1941) presented valuable information on phenology and plant growth from north eastern Greenland. Flowering of many species started in mid-June, earlier than can be observed on islands of the Canadian High Arctic. He also collected considerable information on shoot and leaf growth and overwintering strategy. *Saxifraga oppositifolia* leaves live for two seasons and the development of a *Carex nardina* shoot takes 3-7 years or more. *Dryas octopetala* produces 2-3 foliage leaves per season but Sørensen doubted that *Dryas* leaves overwinter because he observed their withering in fall. He did not realize that some of these leaves turn green the following spring and carry on photosynthesis.

Phenology of plants from Bylot Island (73°N), south of Devon Island, was published by Drury (1962), and from Ellesmere Island (Lake Hazen area, 81°49'N) by Savile (1964). In 1962 *Saxifraga oppositifolia* was in flower June 7, and *Dryas integrifolia* June 15. This is almost a month earlier than was observed in Truelove Lowland (75°N) in 1972, an unusually late season, and about 2 weeks earlier than in the other years of this study.

Much information on phenology was published by Russian authors. Shamurin (1966) presented numerous phenology diagrams of the plants of *Dryas* communities in the Tundra of North Yakutia (71°36'N). *Dryas octopetala* reached peak flowering at the beginning of July. He also correlated flowering intensity and duration with microclimatical factors such as air, temperature, relative humidity, and site isolation.

The observation that phenological events of arctic plants differ in timing according to the habitat and exposure from snow was mentioned by several authors. On Spitsbergen (Acock 1940) flowering of dry fjaeldmark species was advanced 14 days compared to other island localities. Especially peak flowering of *Saxifraga oppositifolia* was shifted according to snowmelt. Also Drury (1962) emphasized the regional and microtopographic differences as the primary factor controlling vegetation, its distribution, pattern and phenology. In the Truelove Lowland, Teeri (1972) recorded pattern of flowering of *S. oppositifolia* populations in six raised beach microsites. His data show a gradual shift in flowering pattern between the crest and late snowbed from June 15 to August 15.

In 1972 the author noticed a remarkable shift in phenological events on Ellef Ringnes Island, King Christian Island, and especially on Melville Bay, Cornwallis Island. In mid-July when Devon and Cornwallis Islands were in the process of snow melt, and mostly under cloudy skies, the western Queen Elisabeth Islands had already been snow-free for 7-10 days and numerous species were in full bloom. At the same time Pattie and Babb (personal communication) collected vigorous specimens of *Salix arctica* with fully developed foliage and other species in full flower near Eureka, Ellesmere Island. The thickness of *S. arctica* stems attests to a summer climate more favorable for growing plants in the northern part of the Canadian Archipelago compared to its central part.

In this study measurements are presented on flowering intensity and flowering potential per unit of plant cushion of two species in two different habitats (Fig. 20, 21). Hocking (1968) presented extensive

information about the progression and intensity of flowering per unit area and related flowering to nectar production. *Saxifraga oppositifolia, Dryas integrifolia, Salix arctica,* and *Cassiope tetragona* were studied by Hocking in the years 1963, 1966 and 1967. His results showed marked differences in timing, duration and intensity of flowering as well as differences between the years. Also Gavrilyuk (1966) was concerned in the problem of duration of individual flowers. On the Chuckchi Peninsula, U.S.S.R., the duration of individual flowers varied according to the time of flower initiation and habitat, a phenomenon observed also by the author. Gavrilyuk also gave important information and illustrations on flower morphogenesis.

In recent years the study of phenological events is more and more exploited in production studies. Arkay (1972) noticed the size-age relationshio of *Saxifraga oppositifolia* clumps from habitats with various moisture regimes on Cornwallis Island. This question showed to be quite essential in our production study of cushion species. Callaghan (1971) developed a method of production estimates based upon phenology and growth measurements of individual plant parts and organs (leaves, stems, tillers, etc.). This method is promissing in overcoming some of the problems connected with simple harvesting techniques on an area basis. It has, however, some difficulties too; how to relate production per individual to production per unit area.

Breaking of dormancy

Breaking of dormancy and the subsequent photosynthetic response were studied on *Dryas* and *Saxifraga*. Plants collected in late August 1970 were transported south in insulated boxes, wrapped in plastic bags to avoid drying and stored in a freezer for seven months. The woody

Dryas and the herbaceous *Saxifraga* were studied and compared in order to find out what time factor is involved between snowmelt, breaking of dormancy, and full photosynthetic activity.

Methods

Potted, frozen plants were placed in cylindrical cuvettes (manufactured of a clear, 10 cm internal diameter, plexiglass) with clear plastic bottoms and lids, and sealed with terrostat (Fig. 29). Six cuvettes were used, each containing one pot with experimental material:

Dryas integrifolia - continuous light - 2 cuvettes

Dryas integrifolia - continuous darkness - 1 cuvette

Saxifraga oppositifolia - continuous light - 2 cuvettes

Beach ridge soil without plants and roots - 1 cuvette

The soil was sifted through 2 mm mesh sieve.

Air taken from the building air supply with a known content of CO_2 was purged through all sealed cuvettes and samples of the air from individual cuvettes were periodically analysed in the IRGA set up described in Fig. 30. Net assimilation was measured with a "LIRA" (Model 200) infra-red gas analyser (Mine Safety Appliances Co. Pittsburgh), and recorded. The net assimilation was calcualted using the formula after Šesták *et al.*, 1971:

$$Co \cdot \frac{K \cdot (273 + \text{absolute leaf temp}) \cdot \text{flow rate}}{\text{dry weight of plant (leaf) in grams}} = \text{mg } CO_2 \cdot g^{-1} \cdot h^{-1}$$

Co = IRGA measured ppm (= of CO_2 concentration)

$$K = \frac{\text{molecular weight of } CO_2}{\text{molar volume}} \text{ . hour (in min) . Vol (in litres)}$$

$$K = \frac{44}{22{,}414} \text{ .60 . } 10^{-3} = 0.11778 \text{ . } 10^{-3}$$

Leaf temperatures were measured with copper-constantan thermocouple (0.003 mm).

Under continuous light (fluorescent tubes plus 3 incandescent 100 W bulbs; 1600 ft c = 260 Microeinstein m^{-2} . sec^{-1} cuvette light intensity) the experiment was started with a -8.5°C chamber temperature. Leaf temperatures were 3 to 6°C higher than that of the growth chamber except for the plant kept in continuous darkness. Here leaf temperature was about the same as that of the growth chamber. The plant growth chamber was a "step in" M-12 Environmental Growth Chamber Co. with a temperature range of -20 to +35 ± 0.5°C and controlled relative humidity.

In one and two day intervals the chamber and consequently also the cuvette temperature was gradually raised by 1°C so that at the end of the experiment (after 40 days) the temperature of illuminated plants was 22°C.

Technical problems with frost accumulation when temperatures were below the freezing point, and later problems with water condensation in cuvettes and tubing system caused a high fluctuation in CO_2 measurements.

Results

Dryas integrifolia: Leaves of dormant *Dryas* clumps were brown when

a.

b.

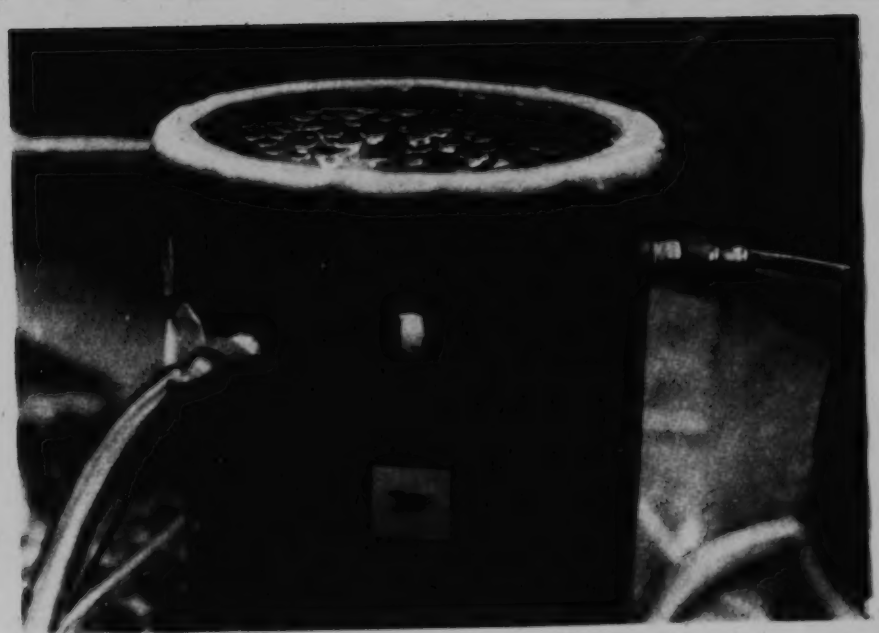


Figure 29. Plexiglass cuvettes with *Saxifraga oppositifolia* (a) and *Dryas integrifolia* (b) plants inside a plant growth chamber.

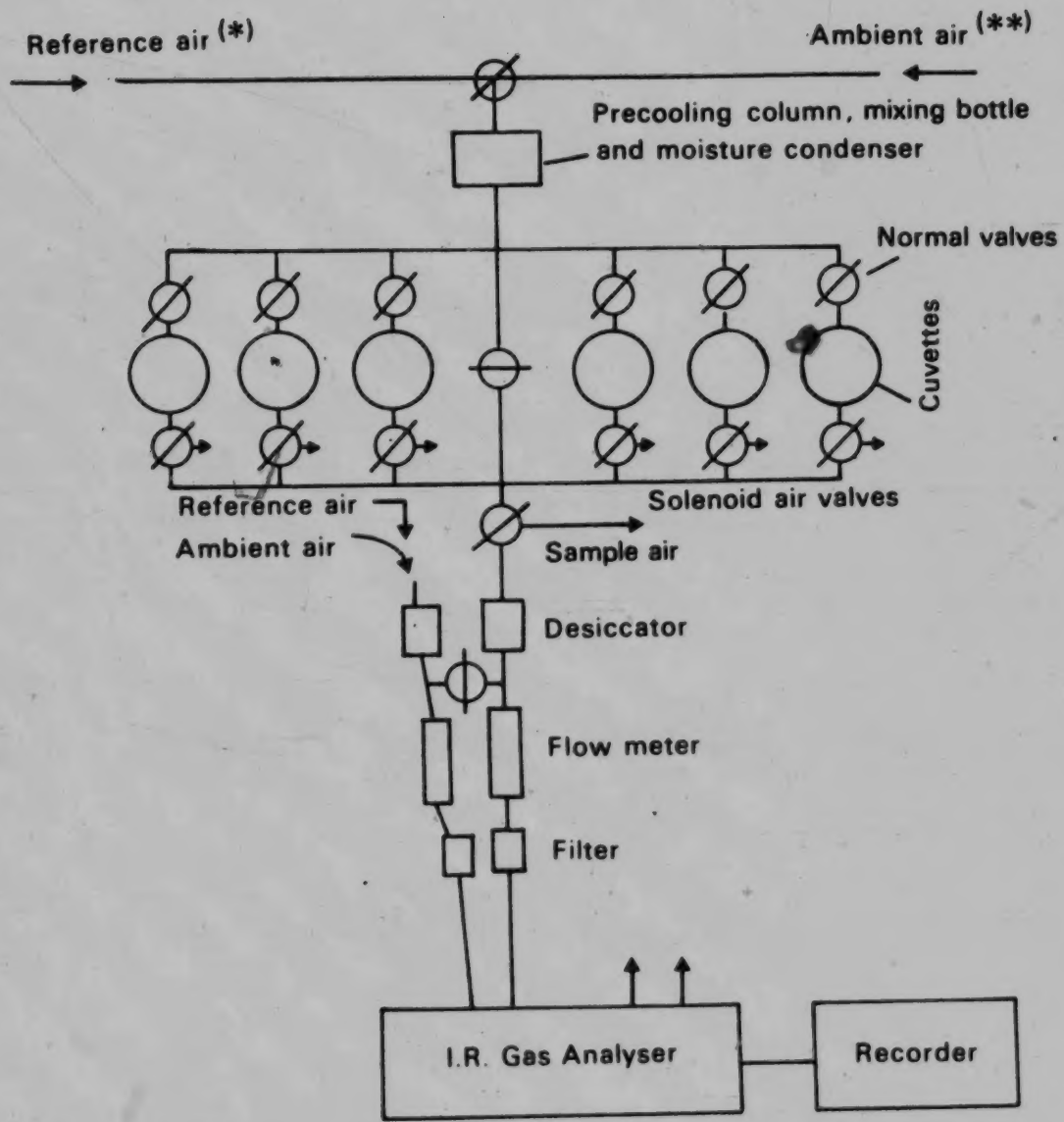


Figure 30. Infrared gas analyser and control system. (*) Reference air of exact and known CO_2 concentration used to calibrate the (**) ambient air. Ambient air was taken from the laboratory air supply.

the plants were placed in the growth chamber, and changed to reddish brown and later to green in a period of approximately 20 days. At the same time, leaf elongation began, increasing in length with time and temperature. All three plants showed the first marks of physiological activity after 10 days of exposure to the changing unvironmental conditions (Fig. 31). Respiratory activity of *Dryas* #3 kept in darkness (Fig. 33a) started at -1 to -2°C, however, respiration was very low. In light treated plants, uptake of CO_2 was not recorded before leaf temperatures reached 1 to 3°C. From this point photosynthesis increased with rising temperature. Two variables, temperature rise and new leaf development, both contributed to increased rates of photosynthesis.

Plant #1 had higher rates of photosynthesis than Plant #2. This may have resulted from differences in non-green:green ratios of both plants. The ratio was 5.50:1 for Plant #1 and 6.12:1 for Plant #2. The evidently greater amount of non-productive but respiring live biomass present in Plant #2 probably influenced the final net photosynthetic balance of this plant. None of the tested plants flowered.

Saxifraga oppositifolia: Plant activity was first observed on day 5 after the plants were transferred to the growth chamber, when the first developing flower buds could be recognized on Plant #2. Plant temperature was about o°C at this time. A positive net photosynthetic rate was recorded between 6-8 days when plant temperatures were slightly above 9°C; rates rose sharply after this (Fig. 32).

Plant #1 did not flower and its net photosynthesis rose exponentially during the whole period of the experiment. It set new green leaves and these developed and expanded rapidly.

Plant #2 gradually developed 13 flowers. This plant showed a

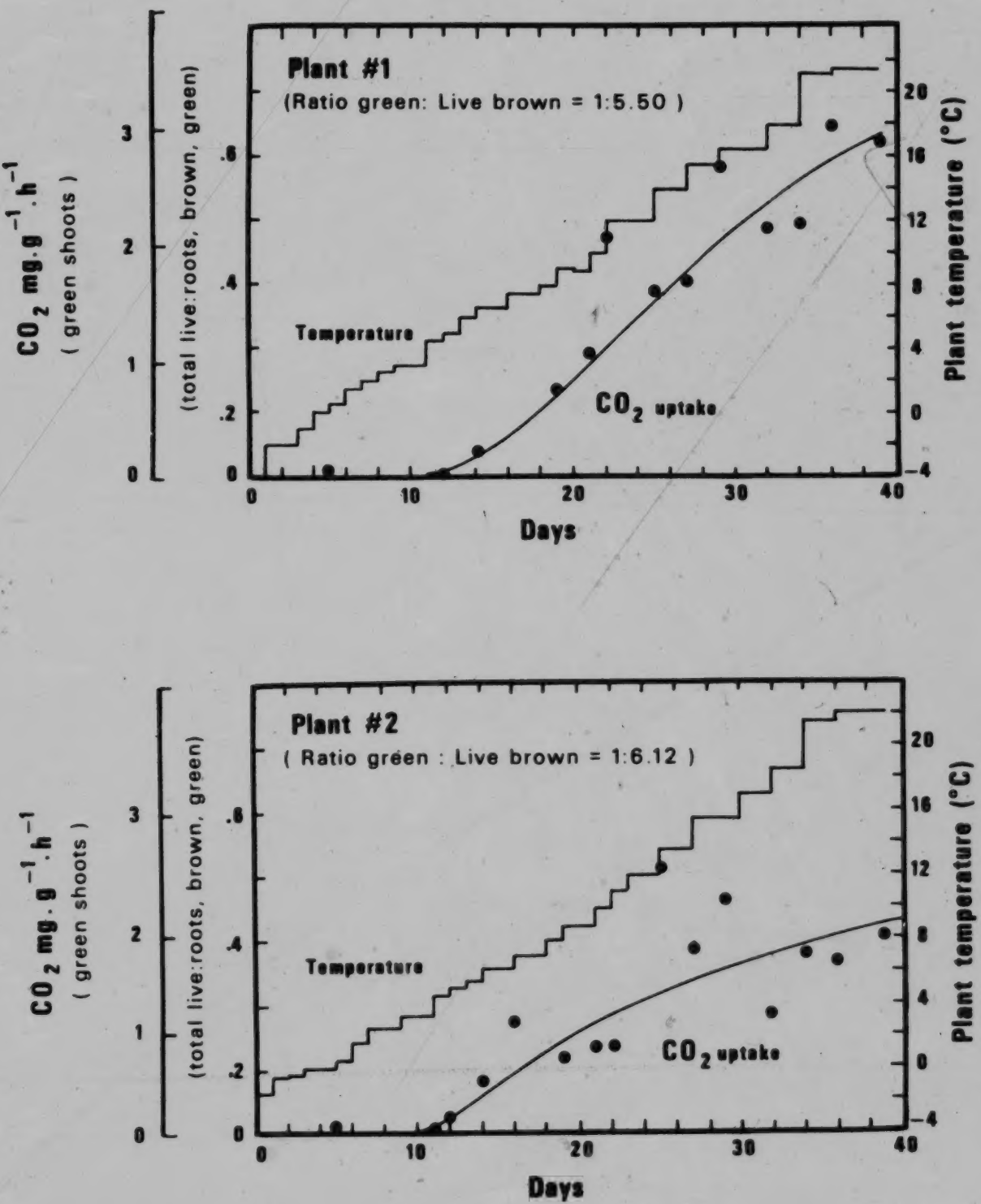


Figure 31. Net assimilation of *Dryas integrifolia* in relation to temperature and days from the start of the experiment with dormant plants. Light level was held constant (260 micro-einsteins . m^{-2} . sec^{-1}).

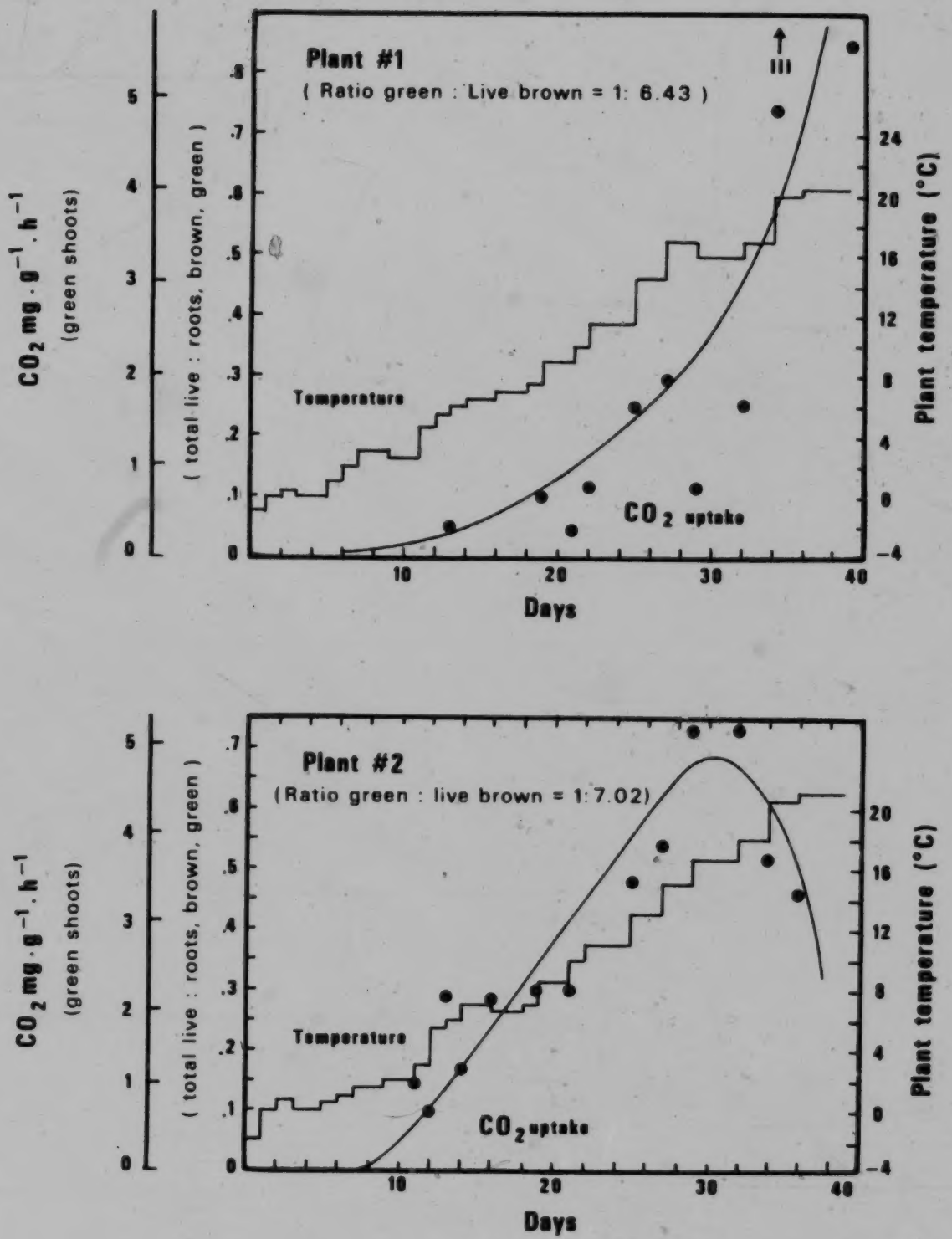


Figure 32. Net assimilation of *Saxifraga oppositifolia* in relation to temperature and days from the start of the experiment with dormant plants. Light level was held constant (260 microeinsteins . m^{-2} . sec^{-1}).

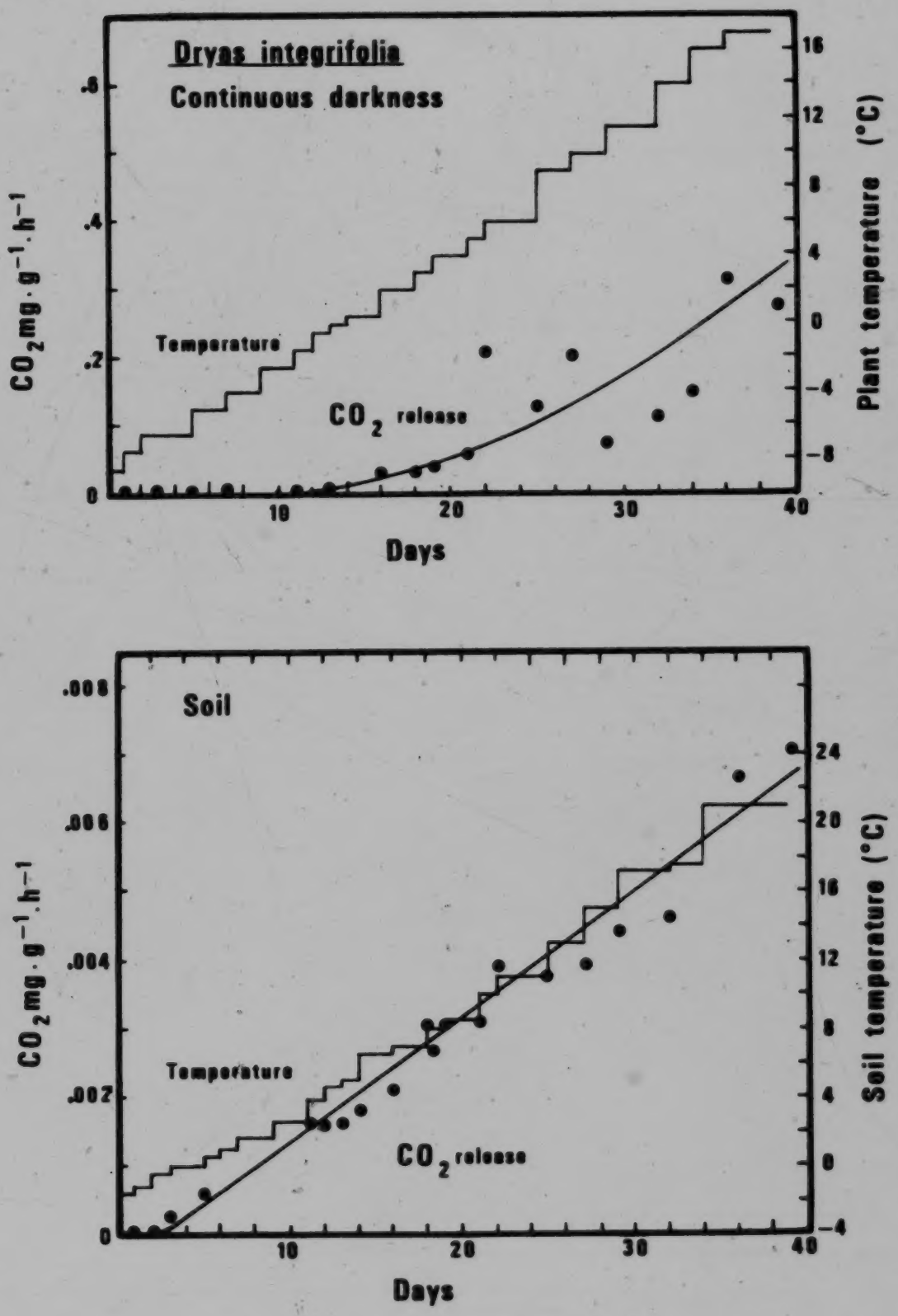


Figure 33. Rates of respiration for a *Dryas integrifolia* plant, and a soil minus plant system in relation to temperature.

sharp photosynthetic rise while in flower. After flowering, however, net photosynthesis dropped progressively. This plant probably reached the predormant state when respiration was still high although net assimilation dropped slowly and ultimately reached zero.

Soil

Respiration of the top soil collected on the crest of IRB showed a close correlation (Fig. 33) with temperature. At 0°C respiration rates were 0.001 mg CO_2 . g^{-1} . h^{-1} and at 23°C the rate was 0.007 mg CO_2 . g^{-1} . h^{-1}. If the soil-plant system is measured, soil respiration can be considered less significant because of the low release rates at the low temperatures used.

Discussion

The results of the growth chamber experiment suggest that:

a. *Dryas* breaks dormancy when the plant temperatures are still below freezing (-1° to -2°C). Positive photosynthetic balance was recorded at leaf temperatures of 3-4°C following 10 days of continuous light treatment and gradual temperature rise.

b. The rate of net photosynthesis per gram of green dry foliage depends on the ratio of non-green:green live biomass of the cushion, and this ratio changes with the age of the cushion. Young plants will have a more favorable ratio which will result in more vigorous growth while old clumps with a higher non-green component will finally stop growth almost completely.

c. *Saxifraga oppositifolia* breaks dormancy much sooner. Flower initiation was observed after 5 days of cuvette treatment and respiration

was measured at temperatures of -2°C, virtually from the beginning of the experiment. Net photosynthesis took over from day 6 when leaf temperatures were slightly above 0°C.

d. The rates of net photosynthesis were higher in *S. oppositifolia* compared with *Dryas*, (2-3 mg CO_2 . g^{-1} green tissue in *Dryas* and 5-7 mg CO_2 in *Saxifraga*).

e. The seasonal cycles of both tested species differ. *Dryas* proved to be a more conservative plant. It broke dormancy more slowly, developed its photosynthetic apparatus gradually and its growth was continuous over the whole season (50-60 days). *Saxifraga* started growth abruptly after snowmelt with a ready green shoot complex which expanded rapidly. It reached the peak of seasonal development soon and in flowering plants the postflowering stage was characterized by a sudden decline in net photosynthesis. The non-flowering clump maintained a higher net photosynthetic rate indicating the energy drain of flowering and fruiting.

The results of the growth chamber experiment complement the overall picture of the behavior of these cushion plants, and agree with the data of Mayo *et al.*, 1973 and Thompson *et al.*, 1973 on *Dryas* assimilation measured in the field in 1971 and 1972 (3-5 mg CO_2 g^{-1} . h^{-1}). The authors also obtained lower values for "red leaved" *Dryas*, shortly after snowmelt. Dark respiration rates measured under artificial conditions are comparable with the field data as well (ca. 2 mg CO_2 g^{-1} . h^{-1} at 20°C). However, Hartgerink (1974) recorded positive CO_2 fixation of non-dormant *Dryas* plants at -4.6°C in the laboratory under controlled environmental conditions. She found the maximum net assimilation (13.4 mg .g^{-1} . h^{-1}) at 15°C. At 24°C net assimilation was almost zero due to high respiration.

The measured progressive start of *Saxifraga* plants immediately after snowmelt is supported by the common observation that *Saxifraga oppositifolia* is the first flowering plant in the High Arctic. Similar field measurements were done by Teeri (1972) who found that most of the initial dry weight gain in *S. oppositifolia* occured while the plants were totally immersed in meltwater.

Vascular Plant Production

The need to collect quantitative data on plant growth and production was emphasized by Blackman (1919) and Boysen-Jensen (1932) early in this century. It took almost 40 years before new quantitative methods were developed and new concepts defined.

Plant production study in arctic and alpine environments was initiated by Bliss (1956, 1962a), Warren Wilson (1960, 1964), Billings and Bliss (1959).

Russian authors have been engaged in arctic ecological problems for a long time. Their main interest was concentrated on phytocoenology and soils as mentioned in previous sections. In the past 15 years Lavrenko *et al.*, (1955), Aleksandrova (1958, 1969, 1970), Chepurko (1966), Khodachek (1969), etc. have published very useful data about the standing crop and zonation of tundra vegetation. In these papers the production and productivity mean standing crop. Real data on arctic tundra production and production rates (productivity) have not appeared in the Russian literature until recently (Chepurko 1972, Gorchakovsky *et al.*, 1972).

The present International Biological Program (IBP) has indisputable merit for encouraging studies of production and productivity of the main world biomes including the Tundra Biome. Of the tundra

biome studies within the IBP only the Canadian Devon Island Project is located in the High Arctic. There are no data in the literature dealing with production of Polar Desert or Polar Semi-Desert plant communities except for indirect estimated.

Methods

1970 growing season

Harvesting for production was done in randomly chosen (5x5 m) subplots. Sixteen samples (20x50 cm) were harvested (two for each subplot) by first digging up the plants with all available roots. The remaining soil containing some roots was dug in two layers (0-10 and 10-20 cm). All collected material was sorted as to species. Each species was divided into roots and shoots, and shoots further subdivided into standing live (brown stems and green leaves) and standing dead. Roots were washed in containers and all floating roots were collected. This way even very fine roots were saved, while carbonized ancient root fragments sank to the bottom. All plant material was ovendried at 80°C. Five harvests were performed on the Intensive Raised Beach during 1970: at 0, 7, 15, 28, 49 days starting June 22. In the fourth harvest special attention was given to the lichen and moss standing crop.

1971 growing season

The second year subplots were chosen by a zonal stratified random technique. Sample size was increased to 1 m^2 to get greater homogeneity in samples. The time span for harvesting was: 0, 7, 14, 28, 49 days (total 49 days) starting June 21.

Procedure of 1971 sampling:

1. One sample (100x100 cm) was randomly chosen in each subplot, 12 per harvest.
2. Total cover of community and cover by species present was determined in each sample.
3. Three randomly selected individual plants (clumps) per each species present in the sample were dug out with the whole root system, labeled and bagged separately for further detailed study (root: shoot, dead:live, brown:green ratios). At each sampling, 30-40 individuals per species were harvested.
4. Remaining aboveground standing crop in the sample was collected and separated by species. The standing crop proportions for green, brown, etc. in the sample were calculated using the ratios obtained from analyses of individual plants.
5. Soil cores (M=120, 6.5 cm in diameter) were collected (10 per each harvested subplot) once during the season in order to estimate the total below ground root and fibrous organic matter.
6. Extensive program: Ten quadrats (50x50 cm) per each zone of 10 additional raised beaches were sampled for vascular plant cover and five of them for the vascular plant aboveground standing crop. Standing crop of the remaining non-harvested five quadrates in a zone was calculated using the regression of cover versus standing crop.

Short methodologic descriptions of snow cover, soil moisture, plant and soil temperature and some other simple measurements are included.

1972 growing season

Harvesting of vascular plants was conducted on an individual plant/species basis; 10-35 individuals per species per zone were harvested along with the root system immediately after snowmelt (Harvest 1), and at the peak of growth for each species (Harvest 2). The area of each plant clump was measured and the standing crop as well as production values per m^2 were calculated using the species cover information in the zone.

Consecutive sampling enabled one to obtain the maximum span between the lowest and the highest dry weights, and allowed necessary time to work on sample separation.

Calculation of production

Values for standing crop vary so much that calculations of seasonal production could not be based on the simple total weight differences between harvests. Green photosynthetic portions of standing crop show the least variation, and were therefore taken as the main criterion for the production estimates.

Aboveground production: Average annual shoot production was calculated by developing and using a laborious technique of *Dryas* aging and the determination of non-photosynthetic stem biomass accumulation in a clump over many years. On average, 2.5 new green leaves are produced per live *Dryas* shoot each year. The total number of dead but still attached leaves on a shoot divided by the average number of new leaves each year (=2.5) gives age and also rate of linear growth of a shoot.

The weight of a dry stem (stripped of all leaves) divided by its

estimated age gives the mean annual dry weight production of a stem. Whether this increment was distributed regularly along the entire stem or used mainly in an apical growth makes no difference in this calculation. This annual stem increment was calculated to be 20.6% of the net seasonal green shoot production. Thus net annual shoot production is calculated by summing net seasonal green production plus an additional 20.6% of this production as assumed to be translocated and used in stem diameter growth.

Belowground production: Net annual root production was assumed to be equal to stem production (also *ca.* 20.6% of the green production) for the following reasons. A *Dryas* stem:root ratio is 1.8:1 (±0.3). This would suggest a higher stem production when compared with roots (only brown stems stripped of all leaves were used in this calculation). Nevertheless, some fine roots are produced and die back each year which are not harvested or are destroyed by washing, therefore it is assumed that root production is about equal to stem production and I have used this ratio in these calculations. Previously (Svoboda 1972) root production was assumed to be double that of brown stem production.

The estimation of active (living) and inactive (dead) roots of *Dryas integrifolia* was based on the use of radioactive phosphorus in the field. Shoots were labeled with ^{32}P, and after allowing two days for translocation to the roots, autoradiographs were made to distinguish live (translocating) from dead (non-translocating) roots. This technique is described by Svoboda and Bliss (1974).

Dryas total seasonal production was calculated by using the formula:

$$\text{Seasonal green production} + \frac{\left[\text{Seasonal green production} \times (0.206 + 0.206)\right]}{\text{stem and root production}} \; (=0.41) = \text{Total seasonal above \& belowground production}$$

Assuming that the strategy of the cushion species is fairly similar, the factor of 0.41 was applied for the calculation of the community production in each beach ridge zone.

Results

Extensive Study Raised Beaches

The results of the extensive sampling program of cover and aboveground standing crop on eleven beach ridges in the Truelove Lowland are presented in Figure 17.

As already mentioned in the section on plant communities, a positive correlation was found between age and elevation of raised beaches, and their plant cover and total standing crop. Older beach ridges which are located further from the shore also have a better microclimatical regime (higher temperature) as was documented by Courtin (1972 and 1973). This has influenced plant establishment, community cover and standing crop. The differences are most pronounced in crest and transition zones while the slopes maintain a fairly constant cover and standing crop. The effect of beach ridge compass orientation and slope angle probably overrule the factor of age, elevation and distance from the shore.

On crests, the aboveground standing crop ranges from 30 to 255 $g \cdot m^{-2}$ (average 97 $g \cdot m^{-2}$). Steep ridges with a narrow crest dry out

quickly, making plant establishment difficult. Some crests remain almost barren. On the other hand, flat ridges resembling a road hold more moisture and therefore a greater plant cover and standing crop develops.

On slopes and transitions the standing crop is 200-480 g m^{-2} (average 287 g m^{-2}) and 165-530 g m^{-2} (average 359 g m^{-2}) respectively. A series of figures (Appendix) presents the linear correlations for individual species of aboveground standing crop vs. plant cover. The figures are based upon 1971 sampling data.

The Plateau.

Cover and standing crop data are presented (Table 8) for two sites on the East Plateau Polar Desert. Vascular plant standing crop is very low here, with mosses comprising the main component. The moss vascular plant ratios are high: 11.2:1 (Area A) and 4.3:1 (Area B).

On the Plateau, *Saxifraga oppositifolia* is the prevalent species and is accompanied by *Papaver radicatum*, *Cerastium alpinum* and tufts of *Poa glauca*. Plants have very tiny thread-like roots and the shoot: root ratio is higher than that on the beach ridge. There were no woody plants present in the areas sampled. Woody species (*Salix arctica* and *Dryas integrifolia*) can be found near the plateau edge but only in small protected habitats.

Production values were found to be very low on the Plateau, 2-5 g . m^{-2} (Table 8). Even these figures cannot be taken as representative for the whole upland Polar Desert where there are waste areas with virtually no plants at all (0 to 3% cover). These data were gathered within 1 km from the edge of the Plateau.

Table 8. Plant cover and standing crop of the Polar Desert Plateau east of the Truelove Lowland, Devon Island, N.W.T.

Species	Area A (1970) Cover %	Area A (1970) $g.m^{-2}$	Area A (1970) % of total	Area B (1971) Cover %	Area B (1971) $g.m^{-2}$	Area B (1971) % of total
Arenaria rubella		0.02±0.0	0.1	0.31±0.1	0.13±0.1	0.3
Cerastium alpinum	0.45±0.1	4.04±1.5	17.1	0.91±0.2	1.17±0.5	2.6
Draba alpina				0.04±0.0	0.19±0.1	0.4
Papaver radicatum	0.40±0.2	1.02±0.2	4.3	0.50±0.1	0.99±0.2	2.1
Poa glauca	0.30±0.2	0.68±0.6	2.9	0.86±0.5	0.54±0.3	1.2
Salix arctica				0.03±0.0	1.25±0.2	2.7
Saxifraga oppositifolia	3.90±1.1	15.67±2.8	66.3	4.79±1.4	39.59±13.2	86.1
Saxifraga caespitosa	0.20±0.2	0.88±0.9	3.7	0.55±0.2	1.39±0.6	3.0
Saxifraga cernua	0.15±0.2	0.38±0.3	1.6	0.06±0.0	0.05±0.0	0.1
Stellaria longipes	0.12±0.2	0.92±0.3	3.9	0.20±0.2	0.45±0.2	1.0
Total vascular plants	5.82±1.2	23.62±3.8		7.98±1.6	52.9 ±16.0	
Total moss		266.0 ±45.5		5.11±1.3	232.0 ±33.4	
					4.30 unidentified roots	
					2.82 unidentified standing dead	

RATIOS:

Vascular plants portions:

Total shoots:total roots 7.7:1

Live shoots:total roots 3.5:1

Live brown:green 1.8:1

Production ($g \cdot m^{-2}$)

Vascular plants	Area A	Area B
Aboveground	2.0	4.5
Total	2.4	5.3

Intensive Study

Standing Crop

Results of 1970, 1971 and 1972 sampling for standing crop on the IRB are presented in Tables 9, 10, 11 and 12.

On a community basis the green-photosynthetic standing crop represents a minimal fraction of the total; *ca.* 1.5% at the beginning of the season to 8% at the peak of growth.

The average shoot:root ratio, if only attached roots are taken into consideration, is 4.7:1. Attached roots represent approximately 20% of the total standing crop.

The average dead:live aboveground ratio is 1.7:1 (only approximately 40% of the aboveground biomass is alive). If unidentified (non-attached) roots which are mostly dead were included, the percentage of live would be even lower.

On a zonal basis the standing crop of the aboveground live portion decreases to the top of the beach ridge along with plant cover. Standing crop shows a maximum in the Slope Zone (Table 13). This is due to the high portion of undecomposed standing dead contained in *Dryas* clumps, which are bigger in the drier Slope Zone than in the moister Transition Zone. The contribution of vascular species is presented by zones in Table 14.

Although *Dryas* covers 28% on the Transition Zone compared to 17% on the Slope Zone, there are only 211 g m^{-2} of *Dryas* standing dead on the transition versus 320 g m^{-2} on the slope. The aboveground dead:live ratio for slope is 3.3:1 versus 1.6:1 in the transition and 2.6:1 on the crest. The low ratio on the crest is necessary to account

Table 9. Mean* community standing crop for the Intensive Beach Ridge Site (IRB) in 1970-1972 (g . m^{-2} ± SE).

	1970	1971	1972
ABOVEGROUND			
Green	29.3± 1.7	19.7± 2.6	24.8± 7.9
Live brown	100.9±14.8	95.8± 2.7	70.6± 4.5
Standing dead	169.0±12.3	179.1±19.6	255.2±20.9
BELOWGROUND			
Attached roots	89.2± 3.2	62.7± 2.3	54.8± 1.4
All roots & Fibric org. matter	795.8	704.4	---
RATIOS			
Total aboveground:			
Attached roots	3.6± 0.3	4.8± 0.3	7.5± 0.4
Total aboveground:			
Total belowground	0.4	0.5	---
Aboveground live:			
Attached roots	1.5 ±0.2	1.8± 0.1	2.0± 0.2
Aboveground dead:			
Aboveground live	1.3 ± 0.1	1.5± 0.2	3.2 ±0.4
Aboveground live brown:			
Aboveground green	3.4 ±0.4	5.1± 0.7	3.1± 0.8
Total aboveground non-green:			
Aboveground green	9.3± 0.7	14.7± 1.4	14.1± 3.7
Total non-green:			
Aboveground green	12.2± 0.9	18.2± 1.9	16.6± 4.4

*Mean values of 5 harvests in 1970 and 1971, and of 2 harvests in 1972

Table 10. Seasonal changes in standing crop (g . m^{-2} ± St. Error, n =16) for the Intensive Raised Beach Site (IRB), 1970

	Date of Harvest				
	June 22	June 29	July 7	July 20	August 8
Standing crop for Community:					
Aboveground green	22.9	30.6	33.4	28.9	30.8
Live brown	69.2	148.4	117.5	98.2	71.1
Abovground live total	92.1±14.7	179.0±36.4	150.9±27.1	127.1±20.2	101.9±17.9
Aboveground st. dead	156.9±38.3	178.4±51.6	149.8±25.5	212.9±37.9	147.4±22.0
Total aboveground	249.0±43.9	362.6±81.7	301.4±45.8	340.7±50.4	250.0±39.5
Attached roots	95.4±21.1	83.0±14.8	81.4±19.1	88.9±13.1	67.6±10.8
Total belowground	361.8	546.9	241.0	255.9	148.9
Total aboveground & attached roots	344.4±58.9	445.6±95.1	382.8±60.4	429.6±59.8	317.6±47.5
Total standing crop	610.8	909.5	542.0	596.6	398.9
Ratios for Community:					
Total aboveground: attached roots	2.6:1	4.4:1	3.7:1	3.8:1	3.7:1
Total aboveground: total belowground	0.7:1	0.6:1	1.2:1	1.3:1	1.7:1
Aboveground live: attached roots	0.9:1	2.1:1	1.8:1	1.4:1	1.5:1
Aboveground dead: aboveground live	1.7:1	1.0:1	1.0:1	1.7:1	1.4:1
Aboveground brown:green	3.0:1	4.8:1	3.5:1	3.4:1	2.3:1
Total aboveground non-green: green	9.9:1	10.7:1	8.0:1	10.7:1	7.1:1
Total non-green:green	14.0:1	13.4:1	10.4:1	13.8:1	9.3:1

Table 11. Seasonal changes in standing crop (g . m^{-2} ± St. Error, n = 12) for the Intensive Raised Beach Site (IRB), 1971.

	Date of Harvest				
	June 21	June 28	July 5	July 19	August 9
Standing crop for Community:					
Aboveground green	13.4	16.3	17.2	24.1	27.5
Live brown	105.0	98.4	89.8	92.6	93.2
Aboveground live total	118.4±21.0	114.7±19.1	107.1±18.3	116.7±22.7	120.7±20.4
Aboveground st. dead	128.1±19.9	153.9±25.1	196.5±32.0	243.2±34.9	173.7±24.3
Total aboveground	246.6±35.5	268.6±34.7	303.6±45.2	360.0±50.5	294.5±39.9
Attached roots	66.0±13.7	62.3± 9.9	68.5±14.1	62.1±11.4	54.8± 9.3
Total aboveground & attached roots	312.6±47.1	330.8±42.8	372.1 54.6	422.1±59.7	349.3±45.5
Total roots				229.5±27.3	
Blgr. fibric org. matt.				474.9±81.6	
Total standing crop				1064.4	
COMMUNITY COVER	28.7	34.7	35.1	39.7	40.4
Ratios for Community:					
Total aboveground: attached roots	4.0:1	4.4:1	5.0:1	5.9:1	4.6:1
Total aboveground: total belowground				0.5:1	
Aboveground live: attached roots	1.8:1	1.8:1	1.5:1	1.9:1	2.2:1
Aboveground dead: aboveground live	1.1:1	1.2:1	1.9:1	2.1:1	1.3:1
Aboveground brown:green	7.1:1	6.0:1	5.2:1	3.8:1	3.4:1
Total aboveground non-green: green	17.9:1	15.5:1	16.6:1	13.9:1	9.7:1
Total non-green:green	22.9:1	19.3:1	20.6:1	16.5:1	11.7:1

Table 12. Seasonal changes in standing crop* ($g \cdot m^{-2}$) for the Intensive Raised Beach Site (IRB), 1972.

Date of harvest	June 29-July 13	July 24-Aug 11
STANDING CROP FOR COMMUNITY		
Aboveground green	16.8	32.8
Aboveground live brown	66.1	75.1
Aboveground live total	82.9	107.9
Aboveground standing dead	234.3	268.5
Total aboveground	317.2	376.4
Attached roots	54.0	55.5
Total aboveground & attached roots	371.2	431.9
COMUNITY COVER (%)	35.69	
RATIOS FOR COMMUNITY		
Total aboveground: attached roots	7.1:1	7.9:1
Aboveground live: attached roots	1.8:1	2.2:1
Aboveground dead: Aboveground live	2.8:1	3.5:1
Aboveground live brown:green	3.9:1	2.3:1
Total aboveground non-green: Green	17.8:1	10.4:1
Total non-green: Green	21.0:1	12.2:1

*Standing crop was calculated by combination of area and crop values of harvested individual plants with the cover values for the IRB

Table 13. Seasonal changes in standing crop (g . m^{-2}) for the three zones of the Intensive Raised Beach Site (IRB), 1972

	CREST		SLOPE		TRANSITION	
Harvest Date	I June 29	II July 24*	I July 4	II July 27*	I July 13	II July 31*
Standing Crop for Community:						
Aboveground green	6.5	17.0	13.9	29.3	35.6	59.5
Live brown	47.8	53.3	83.1	80.9	62.1	94.6
Aboveground total	54.3	70.3	97.0	110.2	97.7	154.1
Aboveground standing dead	149.5	181.2	359.2	370.3	139.0	245.5
Total aboveground	203.8	251.5	456.2	480.5	236.7	399.6
Attached roots	55.5	53.8	56.8	58.3	46.4	53.1
Total aboveground & attached roots	259.4	305.3	513.0	538.8	283.1	452.7
COMMUNITY COVER	19.72		34.95		58.30	
Ratios for Community:						
Total aboveground:attached roots	4.6:1	5.3:1	8.0:1	8.2:1	5.1:1	7.5:1
Aboveground live:attached roots	1.2:1	1.1:1	1.7:1	1.9:1	2.1:1	2.9:1
Aboveground dead:aboveground live	2.7:1	2.6:1	3.7:1	3.3:1	1.4:1	1.6:1
Aboveground live brown:green	7.3:1	4.3:1	6.0:1	2.7:1	1.7:1	1.6:1
Total aboveground non-green:green	22.9:1	18.3:1	31.8:1	15.3:1	5.6:1	5.7:1
Total non-green:green	38.8:1	23.0:1	35.9:1	17.3:1	6.9:1	6.7:1
	C. nardina Aug. 8		*C. nardina* Aug. 11		*C. nardina* Aug. 11	

Table 14. Contribution of main vascular species to the standing crop (by zones) of the Intensive Raised Beach Site (IRB), harvested at the peak growth of the individual species (July 27 to August 11, 1972). Data are expressed as g . m^{-2}.

Species	% Cover	Attached roots	green	Live brown	Standing dead	Shoots total	Total st. crop	% of total
Crest:								
Dryas integrifolia	7.55	12.7	3.6	13.4	93.5	110.5	123.2	47.52
Saxifraga oppositifolia	4.05	8.0	2.1	15.0	28.4	45.5	53.5	20.64
Carex nardina	5.80	15.7	0.4	4.4	24.6	29.4	45.1	17.39
Salix arctica	2.17	18.9	0.1	13.6	3.2	16.9	35.8	13.80
Other species	0.15	0.1	0.1	1.4	0.1	1.6	1.7	0.65
TOTAL	19.72	55.4	6.3	47.8	149.8	203.9	259.3	100.00
Slope:								
Dryas integrifolia	16.68	34.7	20.4	43.0	320.5	383.9	418.6	77.72
Saxifraga oppositifolia	6.28	8.4	6.4	29.6	33.0	69.0	77.4	14.37
Carex nardina	3.96	7.7	1.5	3.6	12.3	17.4	25.1	4.66
Carex misandra	0.48	0.3	0.1	0.2	1.5	1.8	2.1	0.39
Carex rupestris	4.52	0.7	0.1	0.1	0.6	0.8	1.5	0.28
Salix arctica	0.86	6.3	0.4	4.0	2.4	6.8	13.1	2.43
Other species	0.17	0.1	0.4	0.3	-	0.7	0.8	0.15
TOTAL	34.95	58.2	29.3	80.8	370.3	480.4	538.6	100.00
Transition:								
Dryas integrifolia	27.80	23.0	36.6	49.4	210.8	294.8	317.8	70.54
Saxifraga oppositifolia	4.60	3.0	4.4	14.6	9.5	28.5	31.5	6.99
Carex misandra	2.08	2.5	1.4	1.7	9.3	12.4	14.9	3.30
Carex rupestris	13.00	9.9	2.2	2.0	3.6	7.8	17.7	3.93
Salix arctica	1.88	4.1	0.7	6.0	0.9	7.6	11.7	2.60
Cassiope tetragona	7.60	9.7	13.2	20.4	10.5	44.1	53.8	11.94
Other species	1.14	0.8	1.0	0.6	0.7	2.3	3.1	0.70
TOTAL	58.30	53.0	59.5	94.7	245.3	397.5	450.5	100.00

for the fact that *Dryas* clumps are very shallow and prostrate here and easily damaged by frost, drought and erosion. Powell (1961) presented a photographic demonstration of a winter blizzard (January 1958) with erosion of snow drifts exposing the summits of the *Dryas* hummocks in Lake Hazen Area, Ellesmere Island. Many areas of bare ground were exposed by blowing snow and sand.

Another significant trend was found in the increase of aboveground live brown:green, total aboveground:green, and total aboveground and belowground non-green:green ratios along the raised beach gradient (Table 13). The trend of these ratios suggests that there is a higher proportion of non-productive tissue per unit of green-photosynthetic tissue going from the transition to crest, i.e. from the more favorable to the least faborable habitats.

Table 15 gives information on the proportion of vascular plants, mosses and lichens on the IRB which was obtained by analysis of harvest 4 (20 July 1970).

Table 15. Distribution of plant community components on the Intensive Raised Beach, Truelove Lowland.

St. crop components	$g \cdot m^{-2}$	% of total
Vascular plants	596.6	80.1
Mosses	77.3	10.4
Lichens	70.8	9.5
Total	744.7	100.0

For further information on moss and lichen species composition, cover and standing crop distribution in beach ridge zones, see

Pakarinen and Vitt (1973) and Richardson and Finegan (1973), respectively.

Production and Productivity

Seasonal changes of the total vascular plant above and below-ground standing crop show an apparent production of *ca.* 100 $g \cdot m^{-2}$ in 1970 and 110 $g \cdot m^{-2}$ in 1971. This would represent a seasonal dry weight increment of *ca.* 30 and 35% repsectively. These values though carefully measured are too high for a Polar Semi-desert community taking into account the very low photosynthetic portion (4-7%) of its total standing crop, low net photosynthetic rates of *Dryas* (Mayo, *et al.*, 1973) and the small percentage of vascular plant cover (Table 4). Should net annual production be based on weight differences from clipping, in order to obtain a significant resolution between harvests, one must increase the sample size and number of samples beyond the carrying capacity of the study site and beyond the physical ability of the researcher to handle such an amount of work.

In order to make reasonable estimates of net annual production another approach was undertaken as described in the Methods, p 84.

Seasonal production is estimated for each of the vascular plant groups: woody species (*Dryas integrifolia, Salix arctica* and *Cassiope tetragona*), monocots (*Carex nardina, C. misandra* and *C. rupestris*), and forbs (*Saxifraga oppositifolia* and a few other species which give a very low contribution to the total biomass) (Table 16).

Annual net production of the IRB was estimated to be 22.3 $g \cdot m^{-2}$ in 1970, 20.4 $g \cdot m^{-2}$ in 1971 and 22.7 $g \cdot m^{-2}$ in 1972. Daily seasonal productivity values may differ according to the criteria used for the definition of the growing season. The "potential" growing

Table 16. Net annual production of vascular plants on the Intensive Raised Beach Site (IRB) in three consecutive years (g . m^{-2}).

Species	cover %	1970 Shoots	1970 Roots	1970 Total	1970 % of Total	1971 Shoots	1971 Roots	1971 Total	1971 % of Total	1972 Shoots	1972 Roots	1972 Total	1972 % of Total
			g . m^{-2}				g . m^{-2}				g . m^{-2}		
Crest:													
Woody	9.72		Not estimated			3.2	0.5	3.7	56.74	8.4	1.4	9.8	65.35
Monocot	5.80		on a			0.6	0.1	0.7	11.21	1.3	0.2	1.6	10.52
Forbs	4.20		zonal basis			1.8	0.3	2.1	32.04	3.1	0.5	3.6	24.13
TOTAL	19.72					5.6	0.9	6.5	100.00	12.8	2.1	15.0	100.00
Slope:													
Woody	19.54					8.8	1.4	10.3	47.90	13.6	2.3	15.9	71.67
Monocot	8.96					0.6	0.1	0.7	3.60	1.4	0.2	1.6	7.45
Forbs	6.45					8.5	1.4	9.9	48.50	3.9	0.7	4.6	20.88
TOTAL	34.95					17.9	3.0	20.9	100.00	18.9	3.2	22.1	100.00
Transition:													
Woody	37.28					17.8	3.0	20.8	69.30	22.1	3.8	25.9	76.40
Monocots	15.28					2.8	0.5	3.3	10.96	1.7	0.2	1.9	5.80
Forbs	5.74					5.0	0.8	5.9	19.74	5.1	0.9	6.0	17.80
TOTAL	58.30					25.6	4.3	30.0	100.00	28.9	4.9	33.8	100.00
Total Beach Ridge:													
Woody	20.70	13.0	2.2	15.2	68.02	9.0	1.5	10.5	51.52	14.0	2.4	16.4	72.05
Monocot	9.61	1.5	0.2	1.7	7.99	1.1	2.4	3.6	17.54	1.4	0.2	1.7	7.51
Forbs	5.38	4.6	0.8	5.4	23.98	5.4	0.9	6.3	30.94	4.0	0.7	4.6	20.44
TOTAL	35.69	19.1	3.2	22.3	100.00	15.5	4.8	20.4	100.00	19.4	3.3	22.7	100.00

season is that period of the year in which plants theoretically can grow. At Devon Island this is the period from snowmelt to fall when mean weekly temperatures drop below the freezing point. On the Base Camp raised beach, the potential growing season varied in 1970-1972 (Courtin 1973):

1970	June 18 - Sept. 15	79 days
1971	June 12 - Aug. 31	80 days
1972	July 5 - Aug. 17	46 days (with *ca.* 7 days below 0°C in early August)

On raised beaches the "actual" growing season from breaking of dormancy to changing of leaf color in fall is, however, much shorter. Most of the cushion plants complete their seasonal cycle in *ca.* 50 days even though the mean weekly temperatures remain above the freezing point for a longer period of time. Allowing for some subjective error, the actual (active) growing season was determined to be 50 days. This gives more uniform and also more probable productivity values:

Active growing season	Productivity ($g \cdot m^{-2} \cdot day^{-1}$)	
(50 days from snowmelt)	Total	Aboveground
1970	0.44	0.35
1971	0.40	0.31
1972	0.45	0.35

Fluctuations in production within the Crest Zone between seasons can be partially explained by differences in available moisture during the growing season. The crest is the best drained zone where soil water potential often falls below -30 bars (Addison 1971). Moisture is the primary limiting factor here.

Root Autoradiography.

An estimation of active and inactive (dead) roots of some cushion species cannot be made visually. Perennial *D. integrifolia* roots are wirelike, dark and do not change physical appearance whether alive or dead. The tetrazolium hydrochloride test is laborious and I failed to obtain satisfactory resolution with this technique in cushion plants.

The autoradiographic technique (^{32}P) which was first successfully tested on transplanted plants of *D. integrifolia* in the laboratory was used to determine active roots in the field in 1972. It yielded both quantitative as well as qualitative results.

It was found that the majority of attached roots are functional and therefore alive. Only limited amounts of root are produced in these woody species each year yet they are functional for a number of years.

The estimated root production values are included in Table 16. They range from 3 to 5 g . m^{-2} for the total beach ridge but are much lower for the crest.

Discussion

Standing crop.

At present there is more information available about standing crop of high arctic vegetation but production estimates of these remote areas are still very limited. Production data for dry exposed habitats in the High Arctic, similar to raised beaches, are, to our knowledge almost completely missing.

Aleksandrova (1958) estimated the total living standing crop of

polygonal moss-herb tundra to be about 119 g . m^{-2}. Later (1970b) she summarized the amount of aboveground standing crop for High Arctic Polar Desert and Arctic Tundra, along with that of other regions (Table 17).

Table 17. Aboveground and underground standing crop of moss-lichen polygons (Polar Desert in Alexandra Land) and Woodrush-grass-dwarf shrub-moss tundra (Arctic tundra in Greater Lakhov Is.) Condensed data from Aleksandrova (1970a and b).

Plant Component	USSR Polar Desert (g . m^{-2})	USSR Arctic Tundra (g . m^{-2})
Live vasc. plants	35	582
of these aboveground	6	71
of these belowground	29	511
Bryophytes & lichens	123	114
Total live aboveground	158	696
Dead plant parts	161	379
Total live & dead	319	1075
of these aboveground	138	354
of these belowground	181	821

Estimates of belowground standing crop and consequently also of root production are troublesome because of the difficulty in estimating live vs. dead roots, and in sampling error because of the spatial variation in standing crop. This is a problem in all vascular plant studies. In a meadow grown on an old raised beach (Barrow, Alaska) Dennis and Johnson (1970) estimate the ratio of belowground:aboveground standing crop to be 18:1 and total belowground:live belowground to be

2.5:1. Muc (1974) found even higher ratios for Devon Island sedge meadows, values similar to that of Aleksandrova (1958).

On Devon Island raised beaches much larger amount of root biomass was found than could be identified as attached to living plants. The ratio for identifiable (attached) roots to unidentifiable (loose) roots is 1:3.7. The autoradiographic technique provided evidence that the majority of roots connected with the shoot of woody species are alive while the remaining portion of unidentifiable roots represent dead root matter, accumulated over a long period of time (Svoboda and Bliss 1974).

Raised beaches have very little moss and the surface is a "real" ground surface. No problem arises in the determination of "ground surface" here. Nevertheless it ought to be mentioned that the practice which uses the uppermost moss layer as an arbitrary ground surface shifts significatn parts of shoots (often photosynthetizing) into the belowground category and thus changes the real root:shoot ratio. We favor the concept of the "soil surface" as being a boundary between the upper living portion of the moss as was suggested by Aleksandrova (1970a), or the separation of the plant portions using morphological criteria (shoot vs. rhizome or root).

Production

There is no direct data in the literature dealing with annual production of similar High Arctic Polar Semi-desert or Polar Desert habitats. Arkay (1972) did some standing crop and production estimates in the Char Lake drainage basin (Resolute, Cornwallis Is., Canada) which is Polar Semi-desert to Polar Desert in character. On gravel

ridges and south-facing scarp slopes, shoot standing crop was 40-50 g . m^{-2}, with *ca.* 8 g . m^{-2} of shoot production. For estimation of root production (Rp) she suggests the root:shoot ratio (R_b/S_b) assuming that the biomass change per gram of roots (R_p) is proportional to biomass change per gram of shoots (S_p)

$$R_p = \frac{R_b \cdot S_p}{S_b}$$

This assumption can be valid if only live aboveground and live belowground portions are correlated. In Polar Desert plants the amount of standing dead in cushion plants can significantly alter the final estimate.

Gorchakovsky and Andrejashkina (1972) estimated 40.0 g.m^{-2} of above ground production for dwarf-shrub-moss-spotty tundra, and Chepurko (1972) 49.9 g.m^{-2} of aboveground and belowground production for spotted alpine tundra (elevation *ca.* 100 m) in Khibini Mountains, Kola Peninsula. Both studied areas represent low arctic localities.

Rodin and Basilevich (1964) give 0.5 kg . m^{-2} for the total standing crop in arctic tundra with 5 g . m^{-2} of net annual increment. Lavrenko *et al.* (1955) estimated the "gross reserves" of the aboveground vegetation mass in placor* zonal plant communities in the European part of the USSR and Soviet Central Asia to be:

60 g . m^{-2} (40 g . m^{-2} annual increase in aboveground biomass) in arctic "semidesert" (Mixed grass-*Dryas* arctic semi-desert);

---

*the term "placor" is characterized on p. 36

120 g . m^{-2} (70 g . m^{-2} annual increase in above-ground biomass) in arctic tundra (mixed grass-sedge tundra).

There is a big discrepancy between both authors regarding net annual production. Rodin's production estimates are too low and Lawrenko's too high compared with net annual production data presented by other authors.

The USSR IBP Tundra research was conducted on four sites, mainly on the Taimyr Peninsula (72°N). This region is High Arctic by its geographic position but the 10°C mean July temperature, high species diversity (*ca.* 240 species), presence of forest and forest tundra transitions (Matveyeva 1972) demonstrate its low arctic character. The same can be stated about the biogeocoenoses of the Kola Peninsula (Manakov 1972).

Table 18 presents data about standing crop and some net production estimates from several Eurasion IBP tundra sites which might be considered as the closest to our studied sites. Data are compiled from several authors.

Lewis *et al.*, (1972) did comparative studies on plant growth and productivity at Disko Island (W. Greenland 69°15'N) and at a subantarctic station on South Georgia (54°17'S). They tested phytometric species, selected native plants (*Phleum alpinum, Poa glauca, Poa pratensis, Salix glauca, Betula nana, Dryas integrifolia, Vaccinium uliginosum* and some others). The authors used a species technique developed by Callaghan (1971) which is based on the analysis of growth form and morphology of a particular species. The performance of individual plants or plant parts rather than the

Table 18. Standing crop and production (g . m^{-2}) estimates of some Eurasian tundra habitats, compiled from several authors

Author	Locality	Habitat	Total vascular & non-vascular st. crop	Vascular Plant st. crop	Production
Ignatenko *et al.*, (1972)	Ary-Mas Eastern Taimyr	Spotted Tundra	8238	477 shoots 2341 roots	
Shamurin *et al.*, (1972)	Tareya Western Taimyr	Spotted *Dryas* Sedge Mossy Tundra	7219	89 live s. 17 dead 1474 roots	
		Hummock *Dryas* Sedge Mossy Tundra	10442	99 live s. 50 dead 3474 roots	
Pospelova (1972)	Agapa Western Taimyr	Spotted *Dryas* Moss Tundra	1943	74 live s. 11 dead 1739 roots	
Chepurko (1972)	Khibini Mountains Kola Pen.	Spotted Alpine Tundra (Elev. 1000m)	(646)	71 green 99 brown 476 roots	7.3 green 12.8 brown 29.6 roots
Gorchakovsky *et al.*, (1972)	Harp NW Salekhard (Arctic Circle Region)	Dwarf Shrub Moss Spotty Tundra	2860	237 live s. 38 dead 786 live r. 107 dead r.	40 abovegr.
Khodachek (1969b)	Western Taimyr	Hummocky Tundra		98 Abvgr. st.live 46 Abvgr. st.dead 3473 Roots	
		Spotted Tundra		89 Abvgr. st. live 16 Abvgr. st. dead 1431 Roots (patch)	

biomass changes per unit area are measured.

In shrubs and dwarf shrubs the age determination and cateogrization into age classes preceeds the calculation of annual change in weight using the formula:

$$W_{1\,t_o-t_x} = W_w + n.W_{s\,t_o-t_x}$$

Where W_1 = total aboveground live weight through the growing season (t_o-t_x); W_w = aboveground live wood weight at the beginning of the season for particular age class; W_s = mean weight of younger shoot through the growing season (t_o-t_x) and n = number of younger shoots per plant for particular age class.

This technique is fairly precise and permits the estimation of production over a long time for a species. It averages production over several to many years. It is, however, laborious, with less accuracy of present year estimates and has to be modified and adapted for each species. The method does not easily permit estimates of production per unit area.

A production study conducted via individual species has indisputable merit in areas with high variability of plant cover, diversity of species and plant types and where production is very low. The cushion plant-lichen community on raised beaches is such a community. However, it might be difficult to reconstruct community production based on individual plant measurements, per unit area of ground surface.

The combination of both techniques, sampling for cover and standing crop per unit area as well as individual plants with careful

separation for production seems to be the most effective approach and this was also to a large extent utilized in this study.

In three consecutive years I found that net production was low and that it varied little from year to year, although the 1970 and 1971 summers were mild (mean July temperature 4.1 and 3.6 respectively) and relatively long (80 days) while 1972 was cool (mean July temperature was only 1.8°C) and short (46 days).

Of interest is the agreement of net production for the neighboring habitats, frost-boil sedge meadow and raised beach transition. These selected sites (Table 19) actually represent a topographic gradient, with moisture being a limiting factor on both ends: a deficiency on the Plateau and dry beach ridge crest and an excess in the wet meadow.

The belowground production in the sedge meadows is significantly higher (50 to 70 g . m^{-2}, Muc 1973) compared with the raised beach (3 to 5 g . m^{-2}). Sedges (the dominant component of the lowland's meadow communities) show a different growth strategy because they develop an extensive rhizone system. Each shoot lives a relatively short time (3-5 years) and thus the overall turf turnover is faster than in cushion plants on the beach ridge. The cushion plants remain *in situ* for several decades "creating" slowly their own microhabitat and microenvironment. Individual clumps live a very long time, (± 100 years). Even raised beach sedges (*C. nardina*, *C. misandra*) show a tendency to behave like cushion species. Their rhizomes are reduced so that individual shoots grow together and form dense and compact tufts. The survival strategy of these species is demonstrated by the convergent evolution, i.e., by adopting structures

Table 19. Vascular plant net aboveground production (g . m^{-2}) on the topographic gradient Plateau - raised beach - meadow in the Truelove Lowland after Muc (1973) and Svoboda.

Vegetation type	1971	1972
Polar Desert and Polar Semi-desert		
Plateau	2.0-4.5	
Raised beach crest	4.6	12.8
Raised beach slope	17.9	18.9
Raised beach transition	25.6	28.9
High Arctic Meadow Complex (tundra)		
Frost-boil sedge meadow	26.0	28.8
Hummocky sedge meadow	45.0	39.7
Wet sedge meadow	42.5	38.5

typical for the dry raised beach environment.

Community high variability, species diversity and raised beach topographical heterogenity did not permit the use of simple and at the same time adequately efficient methods for determining production. For these reasons my production and productivity values are still close estimates rather than exact figures.

Photosynthetic Surface and Pigments

Methods

Leaf Area Index: Usual planimetric methods (Květ and Marshall 1971) fail in a Leaf Area Index estimation of cushion species such as *Saxifraga oppositifolia*, *Dryas integrifolia* and *Carex nardina*. The laborious but more adequate technique of Thompson and Leyton (1971) was used. Green leaves or shoots were dipped first in adhesive solution and then covered with small Ballotini glass balls. The balls form a uniform layer over the whole surface. The gain in weight is directly proportional to the area covered.

Leaf area was measured on randomly collected green material of a particular species at the peak of the growing season and Leaf Area Ratio (LAR, correlation between leaf area and dry weight of the leaf) was determined. Leaf Area Index (LAI) for species and the total community was calculated on the basis of regularly harvested photosynthetic standing crop using LAR. LAI of some less frequent species was interpolated.

Chlorophyll: Changes in chlorophyll content were followed throughout the 1970 and 1971 growing seasons in *Dryas integrifolia*, *Saxifraga oppositifolia* and *Carex nardina*. Chlorophyll was extracted from green

shoots according to Arnon (1949), and determined spectrophotometrically (Spectronic 20, Baush and Lomb). All data are based upon five replicates. The amount of chlorophyll was calculated using Arnon's formula:

$$C_{a+b} = 20.2 \times OD_{645} + 8.02 \times OD_{663}$$

C_{ab} (chlorophyll) is in units of mg per liter of solution. Further calculations of chlorophyll per unit of fresh weight and per unit of dry weight have been made.

Results

Leaf Area

The concept of leaf area has a metaphoric meaning in describing the photosynthetic surface of high arctic cushion plants. Leaves of these plants are very small and have a variety of forms. For example in tufts (*C. nardina*), rosettes (*S. oppositifolia*), cones (*C. tetragona*) single leaves overlap to such a degree that only a small leaf part is exposed to direct light. The reduced leaf area is evidently part of the survival strategy in Polar Semi-desert and Polar Desert habitats. This results in a smaller transpiration surface which is an important factor in an environment where soil water potential for days and weeks may remain below -30 bars. It also protects green shoots against excessive heating and in this way a leaf of a reduced size is able to maintain tolerable rates of respiration. This is important because during the growing season the light supply is continuous, and the continuous high temperature might seriously damage the plant. *Dryas*, however, has a low compensation point (less than 0.1 ly . min^{-1}), and

maximum net assimilation of this species occurs at leaf temperatures of 8° to 12°C, conditions that prevail at low sun angle (at "night") and on cloudy days (Mayo *et al.*, 1973).

At the raised beach intensive site, green photosynthetic parts represent a minimal portion (4-7%) of the total plant biomass, with only little seasonal change. LAI is unusually low here (*ca.* 0.1), *D. integrifolia* being its main contributor (Table 20). Leaf area duration (LAD) is low and almost constant (Fig. 34).

Salix arctica is the only woody species with thin, prostrate annual leaves. A vigorous root system and a small above-ground portion of the plant enables *Salix* to renew the photosynthetic apparatus every year and to survive even on some crests but with smaller leaves compared with plants from other sites in the Lowland. Table 21 compares three leaf parameters of *S. arctica* from the IRB crest, and the most favorable habitats in rock outcrops. The differences are evident.

Values of Leaf Area Ratio (LAR) (Table 20), are an important ecological parameter. In beach ridge cushion plants they are very low except for *S. arctica* which is a deciduous species. Low LAR's testify to the massive structure and solid architecture of the *Dryas* leaves which are "designed" to sustain them for two or more years and to resist drought, frost, and snow abrasion in winter.

There have been no comparative data available to the author concerning the LAI of high arctic cushion plants. Dennis and Tieszen (1971) presented preliminary LAI values for Point Barrow and Prudhoe Bay sedge-grass communities, being *ca.* 1.0 and 0.6 respectively. Bliss 1970 gave LAI data for alpine communities on Mt. Washington

Table 20. Leaf Area Index (LAI) and Leaf Area Ratio (LAR) of the Intensive Raised Beach Community, 1970

Spec. Total	*D. int.*	*S. opp.*	*C. nar.***	*C. mic.*	*S. arct.*	*C. tetr.*	*O. sp.*
LAI:							
1. .0864	.0385	.0212	.0126	.0032	.0002	.0040*	.0036*
2. .1201	.0658	.0200	.0125	.0032	.0008	.0040	.0137
3. .1360	.0740	.0171	.0122	.0129	.0004	.0140	.0052
4. .1175	.0556	.0108	.0093	.0048	.0109	.0248	.0011
5. .1235	.0605	.0119	.0063	.0164	.0056	.0107	.0030
LAR:							
A/W 39.8	36.7	32.9	104.0	54.4	142.2	33.0*	40.0
W/A 25.1	27.2	30.3	9.6	18.4	7.0	30.3	25.0
Leaf Area percentage:							
100.0	50.7	14.0	9.1	7.0	3.1	11.5	4.6

LAI=leaf area (m^2)/ground area (m^2)
LAR=A (leaf area cm^2)/W (dry weight g)

$$\frac{1}{LAR} = \frac{W}{A} \text{ (here in mg/cm}^2\text{)}$$

Harvest 1. June 22
2. June 29
3. July 7
4. July 20
5. August 10.

*interpolated values
**total leaf area surface (in other species only half of the total leaf area is taken for LAI).

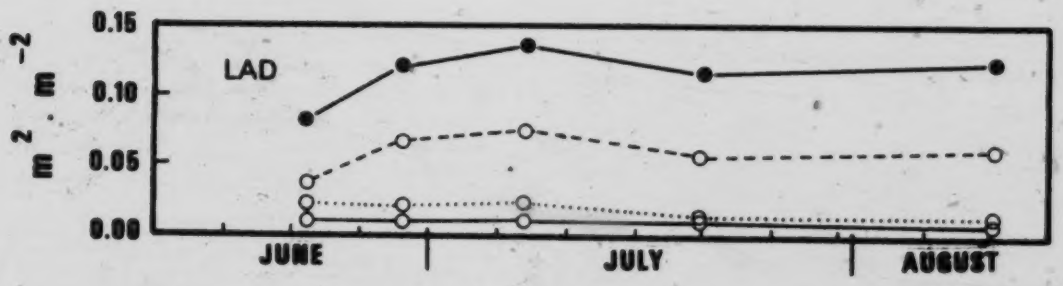


Figure 34. Leaf Area Duration (LAD), of the raised beach community and of the three main species of this community in 1970. ●——● total community; o——o *C. nardina*; o- - -o *D. integrifolia*; o·····o *S. oppositifolia*. LAD = change in LAI during the season.

varying from 0.94 in a heath-rush to 3.30 in a snowbank community, communities with much more structure and production than these on Devon Island.

Warren Wilson (1966) measured several leaf parameters on arctic and non-arctic herbs grown in three latitudes: Cornwallis Island (75°N), Jan Mayen Island (71°N), and Oxford (England) (52°N). Leaf area ratios from two of these sites are presented in Table 22. These data show increasing values with increased nutrient richness of the soil and with decreasing latitude.

Tieszen (1970) measured 43 arctic and alpine grass and herb populations for "density thickness" of the leaves ($\frac{W}{A}$) which is the reverse value of Leaf Area Ratio ($\frac{A}{W}$). The alpine mean $\frac{W}{A}$ value was 0.53±0.03 g . dm^{-2}. The mean $\frac{W}{A}$ value of arctic plants reported previously (Tieszen and Bonde, 1967) was 0.51±0.03 g . dm^{-2}. These values suggest that there is not a big difference between low arctic and alpine populations in leaf area ratio but Tieszen's values are markedly different from our Polar Semi-desert cushion plant values. A mean $\frac{W}{A}$ ratio of 2.5 g . dm^{-2} (Table 20) suggests a very high mass per unit area of leaf).

Similar conclusions can be drawn from the $\frac{W\ plant}{W\ leaves}$ ratios given in Table 13. This ratio as pointed out above (Standing Crop section in this chapter) increases from the Transition Zone to the Crest Zone of the beach ridge where it reaches an extremely high value (23:1) at the peak of leaf development.

Chlorophyll

The pigment study was restricted to basic analyses of chlorophyll

Table 21: Mean leaf length, leaf area, and leaf area ratio (± SE) for *Salix arctica* plants at the Intensive Raised Beach (Crest Zone) and Rock Outcrop east of the Intensive Study Site. Leaf material was collected on July 24 and August 3, 1974, respectively.

Site	leaf length (mm)	leaf area (mm^2)	leaf area ratio (cm^2/g)	(mg/cm^2)
Crest	17.1±0.80	129.8±16.3	142.2	7.0
Rock outcrop	24.6±1.42	192.3± 2.1	132.3	7.5

Table 22. Leaf area ratios (cm^2g^{-1}) of *Oxyria digyna* grown in various arctic soils in pots at Cornwallis Is., and two other forms grown in vermiculite at Cornwallis Is., and in Oxford, England. (Reworked after Warren Wilson 1966).

	Cornwallis Island (75°N)						Oxford (52°N)
Soil:	Barren	Moist sward	Poor marsh	Flower slope	Manured area	Vermi-culite	Vermi-culite
O. dig.	67	81	75	94	101	131	176
P. crant.						121	196
B. rapa						139	319

O. dig. = *Oxyria digyna*; *P. crant.* = *Potentilla crantzii*;
B. rapa = *Brasica rapa*; Vermiculite - non-limiting nutrient medium

$a+b$ and served as a complementary measurement to the productivity study. Absorption spectra of carotenoids are mostly identical with absorption spectra of chlorophylls. Because these pigments cannot be reliably determined without previous separations from chlorophylls, and also because of their high instability the determination of these pigments was omitted in the field work. Results of the analyses, representing woody plants, sedges and herbs are presented in Figures 35 and 36.

The data show a rapid increase of pigments after snowmelt which is followed by a continuous decrease of pigments per unit weight and also per unit area. In both years the trend of seasonal pigment content was very similar, however in 1971 there was a larger pigment standing crop. Beach ridge chlorophyll values did not exceed 3.8 mg . g^{-1} (dry green tissue) in *Carex nardina*, and were lowest in *S. oppositifolia* (1.9 mg . g^{-1}). This is less than Muc (1974) determined for *Carex stans* (8.5 mg . g^{-1}) in meadows, and also less than Dennis and Tieszen (1971) reported for Pt. Barrow Monocots and Dicots (*ca.* 5.0-7.5 mg . g^{-1}).

In contrast to a low but steadily increasing seasonal production, the course of chlorophyll shows a progressive increase to a peak and then a continuous decline. There seems to be a low correlation between chlorophyll content and net production, at least on a community basis. Individual species may show a higher correlation.

Chlorophyll a:b ratios differ between the years 1970 and 1971. The 1970 chlorophyll a:b ratio is higher compared to that for 1971 which maintains close to unity during the whole season, and thus indicates almost an equal proportion of both photosynthetic pigments.

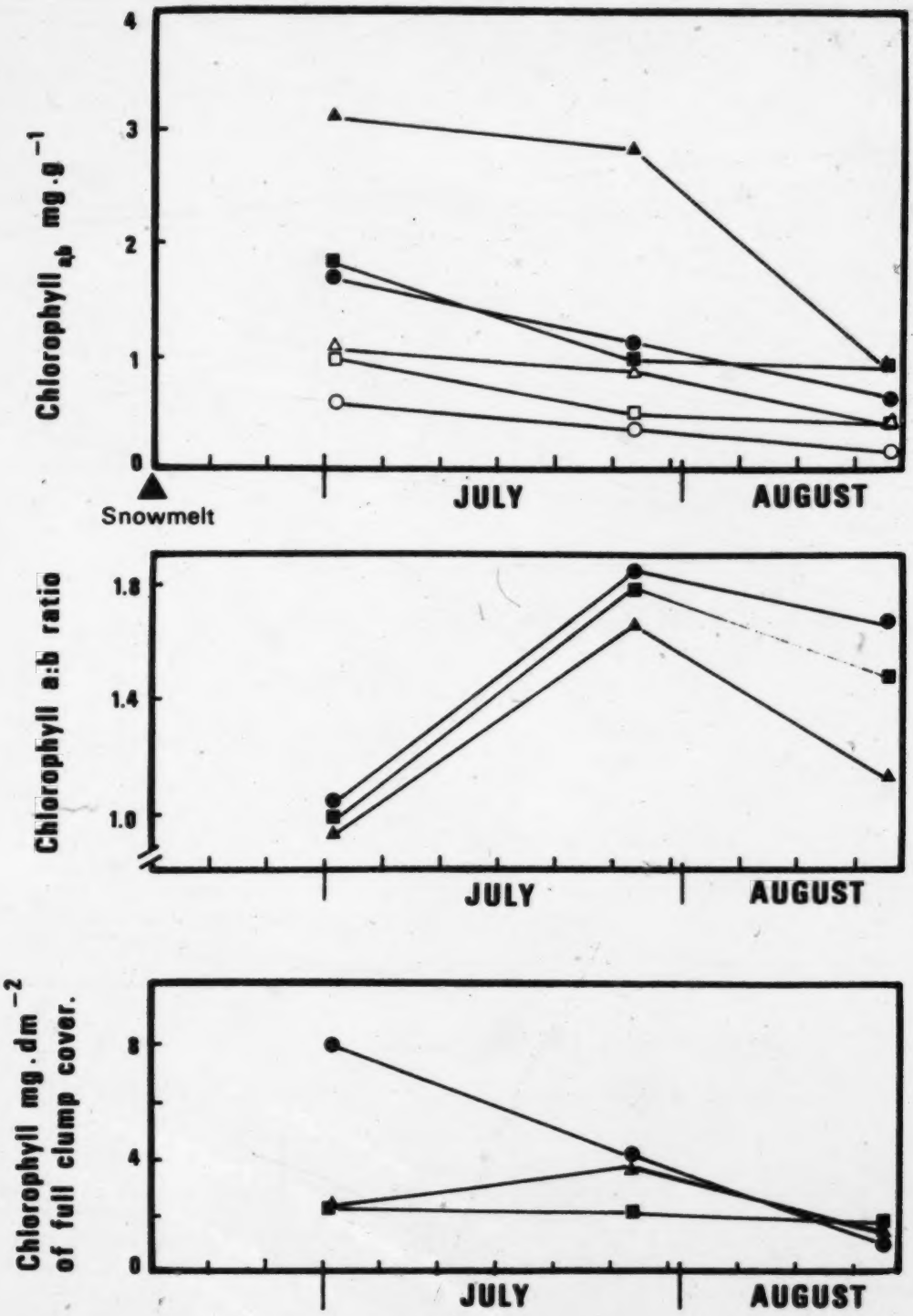


Figure 35. Chlorophyll in *Dryas integrifolia* (■), *Saxifraga oppositifolia* (●) and *Carex nardina* (▲) green shoots on the slope of IRB in 1970. Solid symbols are chlorophyll per gram of dry green tissue and open symbols are chlorophyll per gram of fresh green tissue.

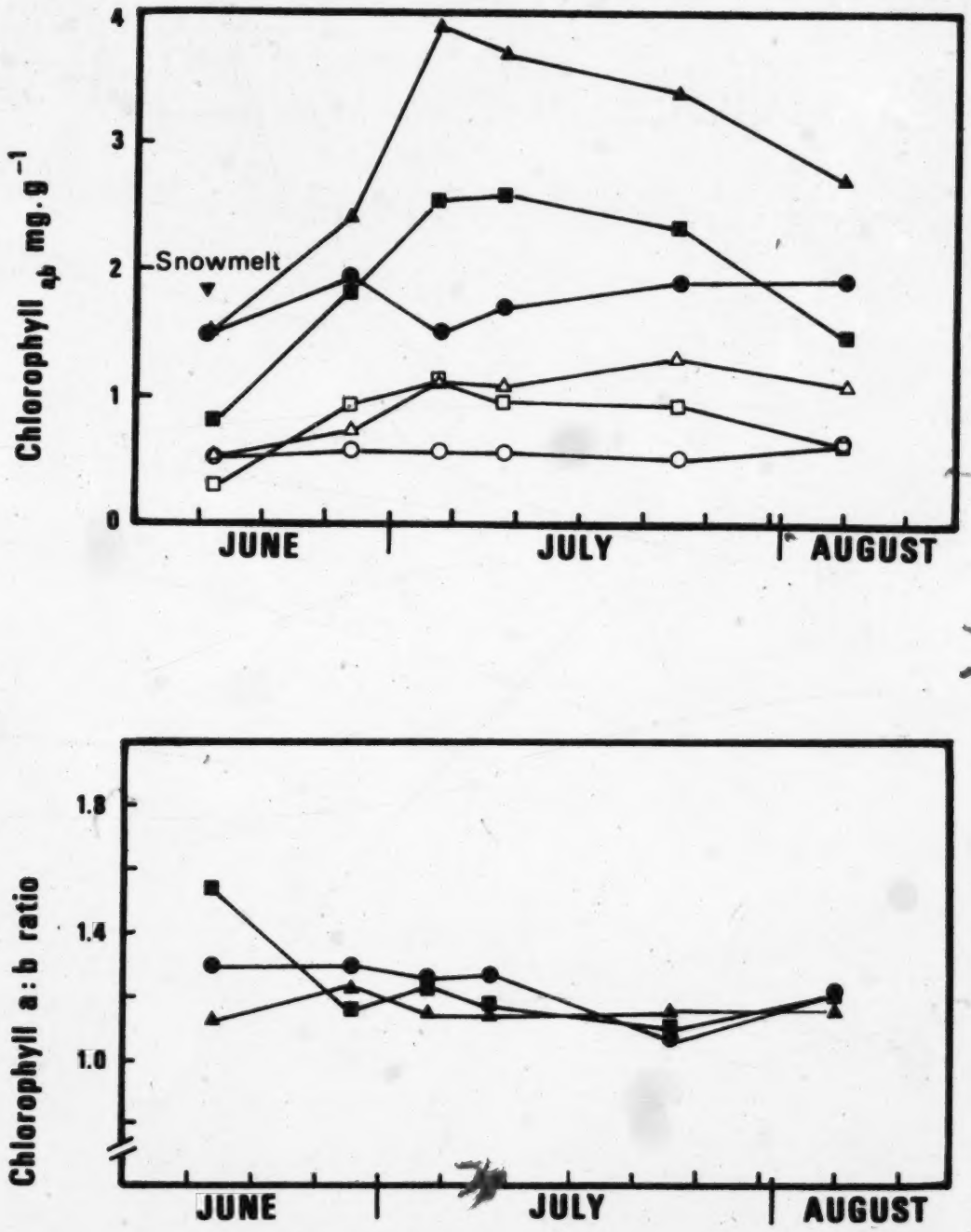


Figure 36. Chlorophyll in *Dryas integrifolia* (■), *Saxifraga oppositifolia* (●) and *Carex nardina* (▲) green shoots on the slope of IRB in 1970. Solid symbols are chlorophyll per gram of dry green tissue and open symbols are chlorophyll per gram of fresh green tissue.

This may be caused by climatic differences between the years. The 1970summer was cooler, with less incoming radiation compared to 1971. If this is the case, we may assume that some of the measured parameters are not genetically fixed but plastic and enforced to a different degree by prevailing microclimatic conditions.

Photosynthetic pigments in arctic and alpine plants attracted researchers looking for anomalies which might be influenced by altitudinal, latitudinal and climatic factors, and they have tried to correlate the biological activity during the growing season with changes in chlorophyll content.

Bliss (1966) estimated the chlorophyll content of various alpine communities on Mt. Washington, New Hampshire:

Heath	0.54 g . m^{-2} (1.91 mg . g^{-1})
Diapensia	0.18 g . m^{-2} (2.69 mg . g^{-1})
Heath rush fellfield	0.62 g . m^{-2} (8.38 mg . g^{-1})

Values in parenthesis - mg . g^{-1} of aboveground standing crop are calculated by the author using the original standing crop data.

Billings and Mooney (1968) postulate that alpine forms have less chlorophyll than arctic forms of the same species whether on a leaf area basis or fresh weight basis, which may be of ecological importance in maintaining tolerable heat balance of the leaf.

Billings *et al.*, (1971) compared the "Photosynthetic number" (=gross photosynthesis in g CO_2 . g chlorophyll^{-1} . h^{-1}) of a series of arctic and alpine populations of *Oxyria digyna* after temperature acclimation. Cold acclimation increased the dark respiration rates in all ecotypes. Maximum rates of net photosynthesis were higher in arctic ecotypes. The authors were convinced that arctic and alpine ecotypes of the same species show not only morphological differences

but are also different ecophysiologically and thus their behavior is under genetic control.

Tieszen and Bonde (1967) and Tieszen (1970) found that after reduction of light intensity, chlorophyll per unit fresh weight increased in *Trisetum spicatum* and *Deschampsia caespitosa*. Populations of arctic species had more chlorophyll than alpine populations under all light intensities. When chlorophyll content was related to leaf area, there was no increase with a reduction of light intensity. A low chlorophyll a:b ratio of arctic species populations (mean value = 2.21) indicated a response to lower light intensity in the Arctic.

Alpine communities on Mt. Washington (Bliss 1966) show chlorophyll a:b ratios ranging from 3.0 to 4.7. Tieszen (1970) points out that the ratios of chlorophyll a:b are low in arctic plants. His figures (Tieszen 1972) for monocots and dicots from Barrow, Alaska (71°N) range from 1.5 to 3.2. This is still high compared to values calculated for cushion plants from Devon Island beach ridges. These range from 0.9 to 1.8 for Monocots and Dicots. At both arctic sites the Monocots show a higher proportion of chlorophyll a.

Tieszen and Johnson (1968), Dennis and Tieszen (1972) and Tieszen (1972) conducted a quantitative and qualitative analyses of pigment structure of arctic tundra communities in relation to above-ground production at Barrow, Alaska. They found that a high correlation exists between chlorophyll content and aboveground standing crop on an area basis with variations between communities ranging from 1.5 mg . g^{-1} (0.32 g . m^{-2}) in dry sedge tundra to 8.8 mg . g^{-1}, (0.77 g . m^{-2}) in Wet sedge tundra. In a dry sedge community about 33% of the total chlorophyll was contributed by mosses.

There was no significant correlation between maximum chlorophyll concentration and dry matter production on a community basis. Dicotyledons showed higher chlorophyll concentration in early spring compared to Monocots. This suggests that different species may have different peaks of chlorophyll and dry matter production which are not synchronized and therefore lower the level of correlation on a community basis. The Mt. Washington (Bliss 1966) and early Alaska (Tieszen and Johnson 1968) work show Monocots have higher chlorophyll than evergreen shrubs which again relates positively to photosynthetic rates, production, etc.

Sestak (1966) sees the problem of apparent non-linearity of the chlorophyll content-photosynthetic activity in variability of ontogenetic factors (e.g. age of leaves). The linearity is limited by the inherent properties of the plant and by the insufficient experimental procedures which according to Sestak are the basic shortcomings of older studies (Gabrielson 1960). Sestak found that correlation is largely improved if the photosynthetic rates are related to chlorophyll a content rather than to the total amount of chlorophyll.

Chemical Composition

Carbohydrates

Methods

Three replicate samples of *Saxifraga oppositifolia, Dryas integrifolia, Carex nardina, Salix arctica* and *Pedicularis lanata* were periodically collected for carbohydrate determination. The sampling program including plant parts analysed for the four years

is presented in Table 23.

Immediately after harvesting the separated and cleaned samples (without standing dead) were put in jars with hot 80% ethyl/alcohol in which a pinch of Na_2CO_3 was added to keep the solution slightly alkaline and prevent spontaneous hydrolysis of non-reducing sugars. The jars were then heated on a water bath for 15 min, sealed and stored for later laboratory analyses.

In the laboratory the solid plant material was separated from the solution, dried at 80°C, weighed and ground to pass a 20 mesh screen. Ground samples (not exceeding 5 g) were extracted on Soxhlet extractors for 6 hrs in a new 80% alcohol solution. The extract was then combined with the original solution, and the insoluble residues were dried and stored for starch analyses.

The alcoholic solution with the extracted soluble plant components was purified by leaf subacetate (Ward and Johnston 1962), filtered and corrected for exact volume. In 1972, 10% of the unpurified extract was taken for evaporation. Dried residue was weighed, and the information on the percentage of total extracted soluble matter was used to reconstruct the true original dry weight of the sample.

Purified solution was analysed with the arsenomolybdate reagent using Nelson's (1944) colorimetric adaptation of the Somogyi spectrophotometric technique for determination of reducing sugars. The carbohydrate determination was done in three steps similarly to that of Warren Wilson (1954):

1. Reducing sugars (monosaccharides) - directly from the purified solution.
2. Total sugars (mono and oligosaccharides) - after mild hydrolysis

Table 23. Sampling program for carbohydrate content in consecutive years (1970-1973), Intensive Beach Ridge Site (IRB).

Species	Sample times during season	Plant Parts: Roots	Live Shoots	brown	Green	Reprod. organs	C	S	T_e	T_l
1970										
Dryas integrifolia	9x	x	x				x			
*Saxifraga oppositifolia**	9x	x	x				x	x	x	x
Carex nardina	9x	x	x				x			
1971										
Dryas integrifolia	6x	x	x				x			
Saxifraga oppositifolia	6x	x	x				x			
Carex nardina	6x	x	x				x			
1972										
Dryas integrifolia	5x	x		x	x	x	x		x	
Saxifraga oppositifolia	4x	x		x	x	x	x		x	x
Salix arctica	5x	x		x	x	x	x		x	
Pedicularis lanata	9x	x	x				x			
1973										
Saxifraga oppositifolia	1x	x					x			
Carex nardina	1x	x	x				x			
Pedicularis lanata	1x	x	x				x			
Oxyria digyna	1x	x	x						x	

C=Crest, S=Slope, T_e=Transition-early snowbed, T_l=Transition-late snowbed

*On July 24, 1970 , *S. oppositifolia* was collected in 5 successive phenological stages starting with dormant plants (late snowbed) and ending on the crest where *S. oppositifolia* was already ripening seeds.

of the sample by 1 N HCl for 20 min in 80°C water bath. Non-reducing sugars (oligosaccharides) were calculated by subtraction of monosaccharides from the total sugars.

3. Polysaccharides (starch) - after the hydrolysis of starch by α-amylase in insoluble residue, and after new extraction on Soxhlet, and purification. α-amylase was used for practical reasons instead of takadiastase suggested in Widdowson (1932) and in Ward and Johnston (1962).

A Spectronic 20 (Baush and Lomb) was used for colorimetric determination of reducing sugars. The 600 nm wavelength proved to have the largest span and gave the best resolution from several other wavelengths tested (500,540, 600,660 nm).

The amounts of carbohydrate are represented in mg . g^{-1} of insoluble residue in 1970 and 1971, and some both in mg . g^{-1} of insoluble residue and mg . g^{-1} of original dry weight in 1972.

Results

The study of carbohydrate activity is an important key in understanding arctic and alpine plant energy and survival strategy and in suggesting the degree of adaptation to extreme environmental conditions. Various aspects of their production, translocation, storage and utilization are the main problems studied.

Dryas integrifolia, *Saxifraga oppositifolia* and *Carex nardina* show very low levels of total carbohydrate reserves in both aboveground and belowground organs. Roots store generally less carbohydrate than shoots and they show also less fluctuation during the season (Figure 37). In all three species, carbohydrates are mostly stored in

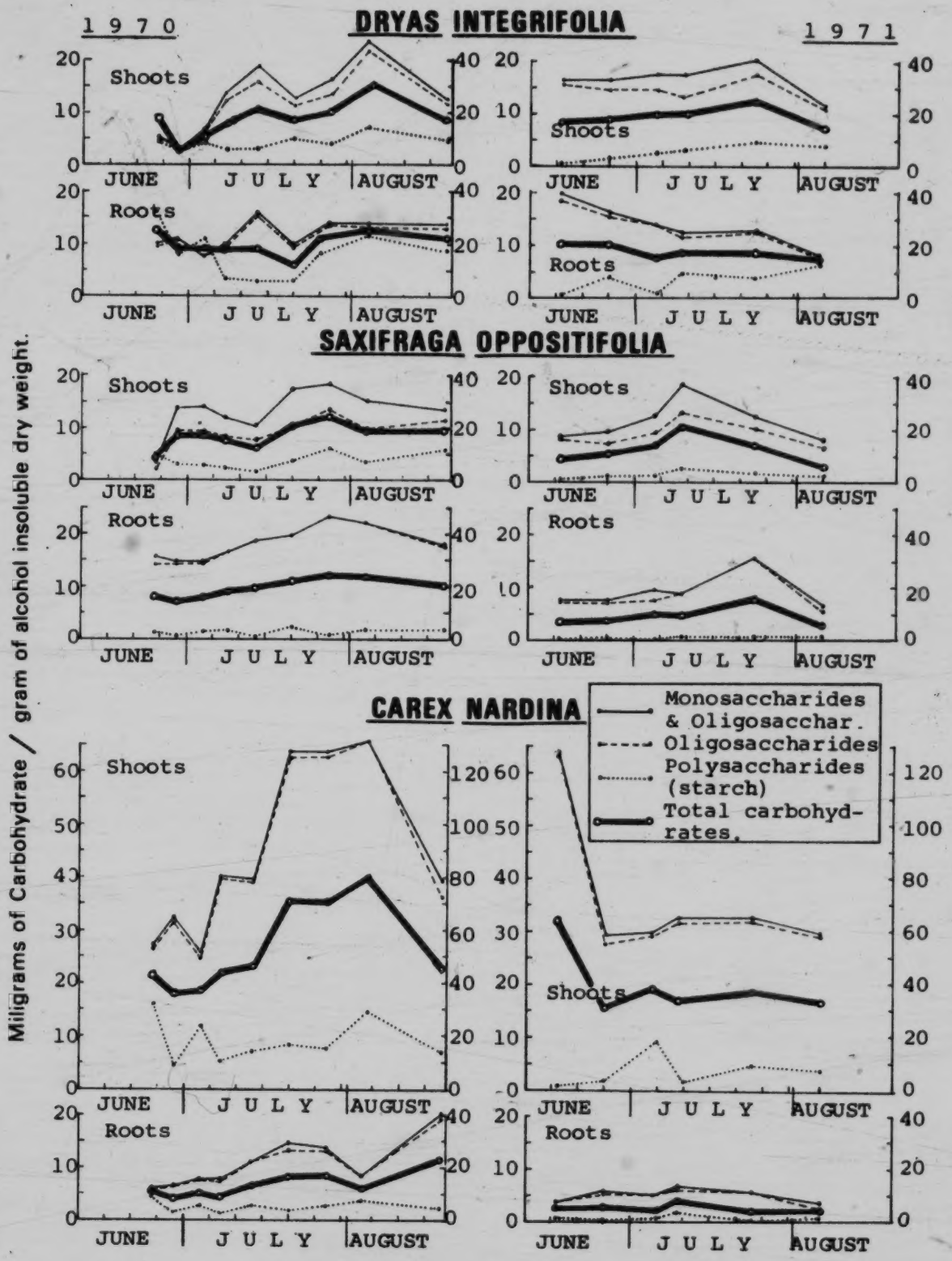


Figure 37. Seasonal changes in carbohydrate content of three species in 1970 and 1971. Right scale total carbohydrates, mg . g^{-1}.

the form of oligosaccharides. The extremely low amount of monosaccharides and low levels of starch represent a peculiarity of high arctic cushion species which live on a very restricted energy budget.

The overall levels of shoot carbohydrate ranged from 0.5-3% in *D. integrifolia*, 0.5-5% in *S. oppositifolia*, and 3-8% in *C. nardina*. Root carbohydrate values were comparable in *Dryas* and *Saxifraga*, but they are significantly lower in *C. nardina*. Green photosynthetic parts contain 2-3 times more carbohydrate than living brown shoots.

Pedicularis lanata was the only true herb species tested which renews the entire shoot every season. Carbohydrate levels (see Fig. 38) were very high when compared with the cushion species mentioned above. Total sugars rise to 17% in shoots and 47% in roots (calculated on the alcohol insoluble residue basis). Also the level of monosaccharides was relatively high. Carbohydrate figures adjusted to original dry weight showed 30-35% lower values (Table 24).

Pedicularis tap roots are morphologically a storage organ evidently loaded with reserves and also the shoots are fleshy, substantially dissimilar in morphology and growth form with cushion species from the same habitat. On the contrary, *Dryas* woody roots and brown shoots are hard and have a very low yearly increment of reserves which suggests that the function of roots and shoots is mainly mechanical and as water and mineral absorbing and transporting organs.

Diurnal changes of carbohydrate level were not studied. The seasonal fluctuation was very low in roots but was found markedly higher in shoots. The mobilization of reserves from shoots is easier in time periods when the shoots are snow-free while roots remain

Table 24. Dryweight percentage of alcohol insoluble residue as compared to the original dryweight of sample before extraction.

Species and Date	Reprod. organs	Green	Upper brown	Lower brown	Roots
Dryas integrifolia					
July 4, 1972			75.9	84.3	89.0
July 21	56.9	86.4	87.4	85.9	89.3
August 8	63.7	71.1	81.9	85.0	87.1
August 8	63.5	69.2	90.3	86.7	90.7
Salix arctica					
June 21, 1972			49.2	75.5	75.8
July 7	89.6	69.1	72.6	81.3	82.8
July 13	75.2	72.6	77.3	83.5	85.2
August 4	71.3	68.6	72.5	79.7	86.4
August 14	70.0	60.2	72.9	82.5	85.2

	Shoots	Roots
*Carex nardina**	88.4	92.5
*Oxyria digyna**	70.7	81.3
*Pedicularis lanata**	73.2	64.5
*Saxifraga oppositifolia**	91.3	95.0

Green = photosynthetic shoots
Upper and lower brown = non-photosynthetic live tops and bases of shoots.
* = collected on August 17, 1973.

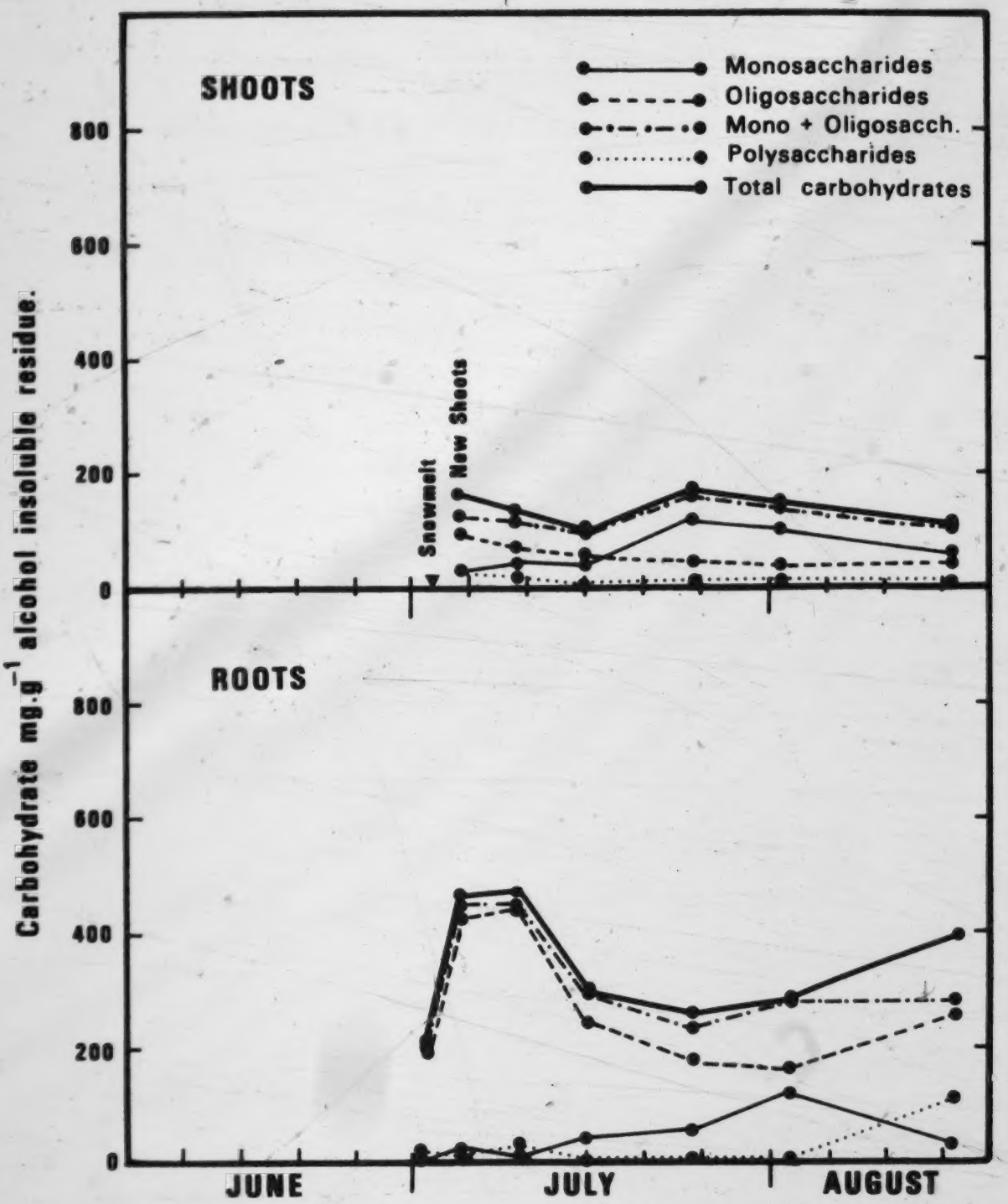


Figure 38. Seasonal course of carbohydrate in *Pedicularis lanata* beach ridge crest, 1972.

frozen or experience much lower temperatures than shoots.

Changes in carbohydrate content are regulated by the phenological stage, photosynthesis, as well as being influenced by the actual weather and microclimate. No significant depletion of reserves has been detected immediately after snowmelt but an increase in total carbohydrate has been found in the middle of the growing season. Root carbohydrate levels copy to a lesser extent the trend in shoots.

Figure 39 presents information on the carbohydrate content of *Saxifraga oppositifolia* along one particular gradient from the Transition Zone up to the Crest Zone. Five sites were sampled, including late and early snowbed in the transition, lower and upper slope, and the crest on July 24, 1970. The plants in the late snowbed were dug out from snow while up slope plants were in successive phenological stages. *Saxifraga* plants on the crest had flowered and seeds were developing (see Phenology Section).

Total carbohydrate content in *Saxifraga oppositifolia* shoots increased up slope until the crest where content sharply declined. There was practically no change in shoot starch levels and very little change in root total carbohydrate throughout all phenological stages and in all five sites.

For a proper interpretation of results it is necessary to realize that two variables were involved, slope position and phenological stage. Fortunately the information on seasonal carbohydrate change in *S. oppositifolia* (Fig. 37) enables us to conclude that slope position determines the overall picture of carbohydrate content more than the phenological stage. Plants growing in the late snowbed have the shortest growing season and cannot always ripen seed. On the other

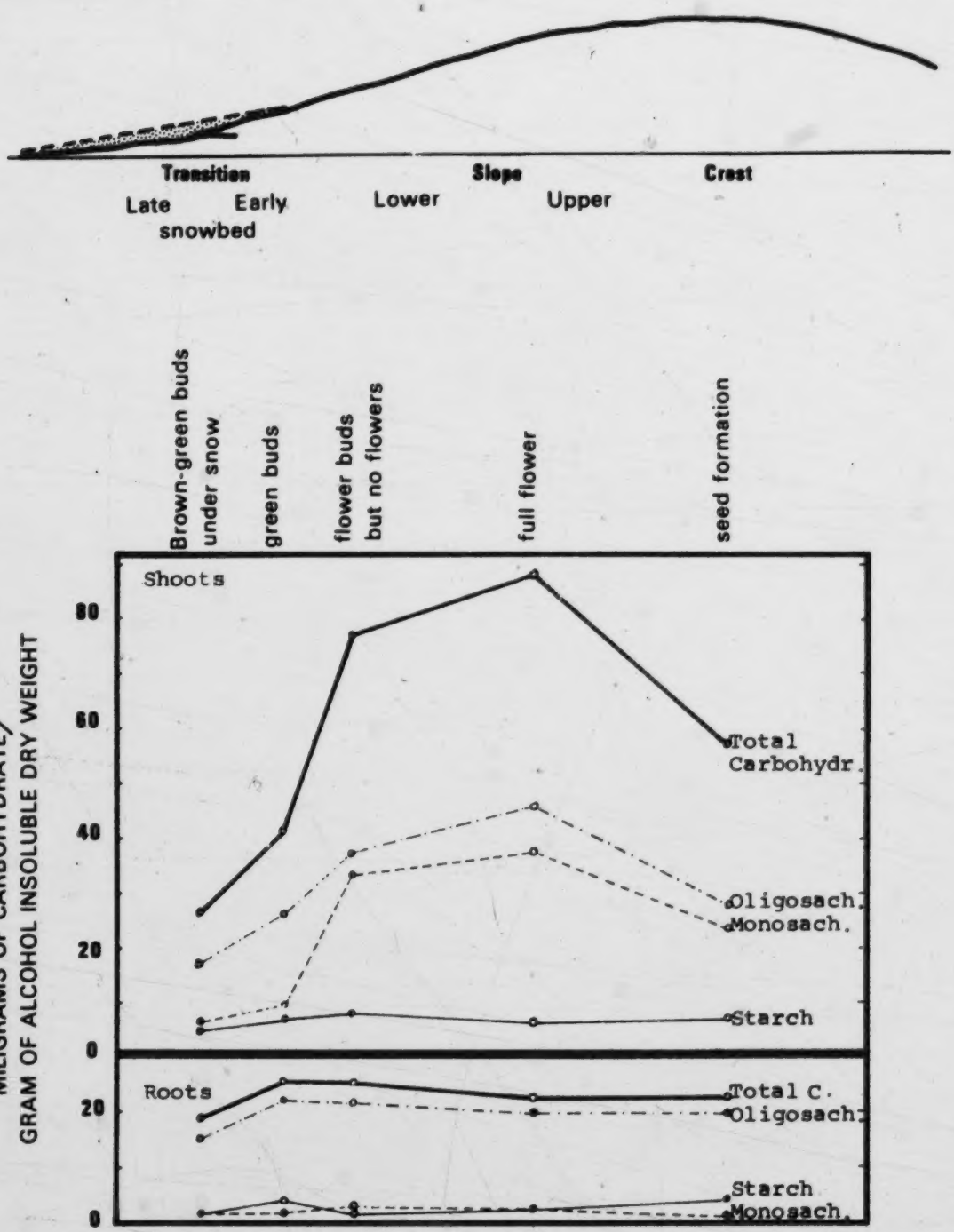


Figure 39. Changes in carbohydrate content in *Saxifraga oppositifolia* according to the position on the slope of the IRB and phenological stage of seasonal development (July 24, 1970).

hand, the crest, which is snow-free earliest, permits early growth, but the long period of extreme soil drought represents stress of another kind. It is assumed (based upon the field measurements of photosynthesis (Mayo *et al.*,1973) that plant respiration rates are sufficiently high to maintain relatively low carbohydrate reserves.

Various ratios of carbohydrate components for beach ridge plants are presented in Table 25. These ratios vary between years but their overall trend shows that cushion species differ from arctic meadow species and also from *Pedicularis* growing in the same habitat.

Relatively low levels of polysaccharide (starch) compared with soluble sugars were found in *Dryas, Saxifraga* and *Carex*. Reducing sugars (monosaccharides) were also a minor fraction compared to non-reducing sugars (oligosaccharides), especially in *Carex nardina* shoots.

Pedicularis lanata is very different concerning the quantity and quality of carbohydrates. Levels of soluble sugars are 10 times higher in shoots and 20 times higher in roots in comparison with cushion species from the crest. The proportions of various sugars are also different. In shoots there are more monosaccharides over the major part of the growing season while roots maintain high levels of oligosaccharides during the entire season. Even here the ratio oligosaccharides:monosacchardies is substantially lower than in cushion plants.

Discussion

a) Carbohydrate levels.

Table 25. Various carbohydrate ratios for four species from the Crest Zone of the Intensive Raised Beach Site (IRB).

Ratios		*Dryas integrifolia* 1970	*Dryas integrifolia* 1971	*Saxifraga oppositifolia* 1970	*Saxifraga oppositifolia* 1971	*Carex nardina* 1970	*Carex nardina* 1971	*Pedicularis lanata* 1972
Starch: total sugars	S*	0.34	0.15	0.29	0.14	0.20	0.10	0.13
	R*	0.65	0.24	0.07	0.03	0.23	0.14	0.09
Oligosaccharide: Monosaccharide	S	7.81	6.89	2.39	3.91	46.56	46.80	0.85
	R	35.03	23.21	51.72	16.35	30.22	13.85	6.54
Oligosaccharides: Total sugars	S	0.88	0.87	0.70	0.79	0.97	0.98	0.50
	R	0.97	0.95	0.98	0.94	0.97	0.93	0.86
Monosaccharide: total sugars	S	0.11	0.11	0.29	0.20	0.02	0.02	0.58
	R	0.03	0.04	0.02	0.06	0.03	0.07	0.13

*S = shoots, R = roots

Ratios calculated from seasonal means.

Russell (1940a,b) suggested that arctic plants produce sufficient amounts of carbohydrate which excludes any starvation. The growth controlling factors are mainly temperature and nutrient deficiency. Mooney and Billings (1960, 1965) found high carbohydrate contents increasing with elevation in alpine vascular plants. Fonda and Bliss (1966) Warren Wilson (1966), Roshchevskaia and Schwetsova (1970), McCown and Tieszen (1971, 1972) and other authors have studied carbohydrate levels in arctic and alpine plants. Some carbohydrate values published by various authors are summarized in Table 26.

It is evident that many arctic and alpine plants maintain high levels of carbohydrate in green shoots and active underground organs. These levels are comparable with carbohydrate contents of plants from temperate zones and sometimes are even higher. Limited growth of cold region plants is not always caused by low photosynthetic rates but rather by limited utilization of produced assimilates due to other environmental and physiological factors as some authors emphasize.

Methodological note: Most authors expressed carbohydrates per unit of "alcohol insoluble residue". The real carbohydrate percentage per unit of original dry weight (and this is the purpose of this study) may be very different as was demonstrated by McCown and Tieszen (1972) and as can be seen in Table 24. Young and soft tissue may disintegrate almost completely during solution storage and after grinding during the extraction (often there is almost no solid residue left) while woody parts will resist disintegration. Not all extracted materials are carbohydrates. The unpurified extract contains virtually the entire cell content (protoplasm and vacuole

Table 26. Carbohydrate values of some arctic, and alpine species compiled from various sources.

Locality	Latitude or altitude	Species	Carbohydrate % Roots Min-Max	Shoots Min-Max	Author
Arctic:					
Jan Meyen I.	71°N	*Oxyria digyna*	40	28	Russel 1940b
		Polygonum viviparum	25	14	
		Ranunculus glacialis		54	
Barrow, Alaska	71°N	*Alopecurus alpinus*		35	McCown and Tieszen 1972
		Arctagrostis latifolia		34	
		Dupontia fisheri		33.5	
Macquarie I. (Subantarctic)	54°S	*Stilbocarpa*	9-65	7.5-11	Jenkin 1972
Alpine:					
Medicine Bow Mountain, Wyoming	3300m	*Saxifraga rhomboides*	8-35	10-45	Mooney and Billings 1960
		Polygonum bistortoides	25-60	10-35	
		Geum turbinatum	20-45	20-30	
Mt. Washington New Hampshire	2000m	*Carex bigelowii*	11-41	18-20	Fonda and Bliss 1966
		Geum peckii	21-34	17-27	
		Potentilla tridentata	10-18	15-25	
		Vaccinium vitis-idea	13-20	24-46	
Wasath Plateau Utah	2700m	*Agropyron trachycaulum*		3.8-18.5	McCarthy and Price 1942
		Bromus carinathus		4.3-14.1	
		Geranium viscosissimum		4.7-19.1	
		Rudbeckia occidentalis		9.7-27.8	

content). Also much starch is washed out of the tissue. The expression of carbohydrate amounts per insoluble residue has only a limited value unless the original dryweight of the sample is known so that the final calculation per unit of original weight can be made.

b) Diurnal and seasonal change

Fluctuation in carbohydrate levels were observed by Russell (1940) and Warren Wilson (1954) on Jan Mayen Island plants. Mooney and Billings (1960) and Fonda and Bliss (1966) described seasonal changes in alpine plants. Arctic monocots (McCown and Tieszen 1971) showed highly synchronous carbohydrate cycles.

Populations of *Caltha leptosepala* released early and late from snowbeds (Snowy Range, Wyoming) had the lowest carbohydrate levels (Rochow 1969). Similarly, Butt (1968) and Eagles (1967) showed that carbohydrate levels depend on temperature and light conditions. McCarthy (1938) observed in *Bromus carinathus* growing at 2700 m (Ephraim Canyon, Utah), seasonal changes not only in soluble sugars and starch but also in levels of hemicellulose.

c) Ratios of carbohydrate components

Ratios of water insoluble (starch:soluble carbohydrate in arctic and alpine plants are considerably lower in comparison with plants from lower latitudes and elevations. In three alpine species transplanted to an elevation below their normal occurence, total carbohydrate, namely starch, dropped progressively (Mooney and Billings 1965). Also *Oxyria digyna* transplanted from Jan Mayen Island (71°N) to Oxford, England (52°N) showed less starch (Warren Wilson 1954). Alpine species (*Pulsatila ludoviciana, Carex elynoides* and *Luzula spicata*) showed mean starch:sugar ratios of

0.39 in shoots and 0.59 in roots (Mooney and Billings 1960). *Carex bigelowii, Geum packii, Potentila tridentata* and *Vaccinium vitis-idea* gave starch:sugar ratios of 0.38 in shoots and 2.07 in rhizomes (Fonda and Bliss 1966). *Carex aquatilis, Eriophorum angustifolium* and *Dupontia fisheri* from Barrow, Alaska and alpine Niwot Ridge, Colorado showed only small differences in starch:sugar ratios (1.71 and 1.32 respectively) for green leaves. Starch in all cases was higher than soluble sugars (McCown and Tieszen 1971).

On Devon Island meadows, *Carex stans* had maximum carbohydrate values of 16% in shoots and 14% in rhizomes and 5% in roots. Starch: sugar ratio was, however, low and constant in shoots (0.05) but increased in roots from 0.01 to 1.1, and from 0.2 to 2.2 in rhizomes during the season (Muc 1972, ratios calculated from Muc's original data by this author). Beach ridge species *Dryas, Saxifraga, Carex* and *Pedicularis* show low starch levels (1 to 2%) and almost constant starch sugar:ratios over the entire season and low variation between years (Table 25).

d) Problem of carbohydrate accumulation.

Neales and Incoll (1968) reviewed the old hypothesis proposed by Goussingault (1868) that accumulation of assimilates may inhibit net photosynthesis of an illuminated leaf. They discussed the work of 89 authors but found no proof that these two phenomena are causally associated. Warren Wilson (1966) discussed this problem in relation to arctic plants because they are supposed to contain high to very high carbohydrate levels which would exclude carbohydrate starvation. This is not always true. The carbohydrate levels of Devon Island cushion and tufted plants are very low. Russell (1940) and Warren

Wilson (1966) based their theory on results obtained on soft herbs (mainly *Oxyria digyna*). Though herbaceous species show relatively high carbohydrate levels, they represent less than 1% of the beach ridge standing crop. Devon Island carbohydrate values for *Oxyria digyna* were *ca.* 18% for shoots and *ca.* 15% for roots expressed per unit of insoluble residue. The true value expressed per original dry weight were only 12.6% (shoots) and 12.1% (roots) which is far below levels critical for photosynthesis inhibition. Also leaf temperatures and respiration rates are not always as low in arctic plants as it is still often assumed.

The seasonal carbohydrate fluctuation especially in shoots of cushion plants does occur, and it is conditioned by phenological stages and the actual environmental conditions. Peaks of carbohydrate follow the phenological sequence of flowering in *Saxifraga, Dryas* and *Carex nardina*.

The overall ratio insoluble:soluble carbohydrate is very low in high arctic cushion and tufted species and supports Eagles' (1967) finding that the proportion of soluble carbohydrate as opposed to starch increases with lower temperatures. The main stored component is the oligosaccharides.

Soft herbs (*Pedicularis, Oxyria, Polygonum, Ranunculus*) show apparently different survival strategy because they renew the entire or a substantial portion of the shoot every year. Carbohydrate levels are relatively high here. The limited distribution of these species on a quantitative basis if puzzling. Most probably this is due to an inadequate adaptation to low temperatures and frost damage.

Slow growth rates and stunted growth forms of high arctic plants

seem to be primarily a result of low temperature. The nutrient deficiency of arctic soils is of no less importance but this phenomenon, namely nitrogen deficiency, is basically also a temperature dependent phenomenon. Low tempteratures in the soil maintain low nitrogen fixation rates (Russell 1940a, Stutz 1973) and nitrogen uptake is not inhibited by cold soils as is the uptake of phosphorus by native arctic species (Haag 1974).

Carbohydrate synthesis seems to function as a continuously running free wheel system where assimilates are produced and consumed almost at the same rate (on a daily basis), a system which is highly inefficient with regard to the utilization of the assimilated product due to the complexity of external and internal limiting factors.

The carbohydrate reserves of polar semi-desert and polar desert cushion species suggest a lot about the degree of stress imposed on these plants by the harsh environment. They live literally "from hand to mouth".

Lipids, protein, fibre, nutrient status

Methods

In the determination of lipids, the methods of Bliss (1962b) were followed. Known amounts of dried and ground material (0.5-1.5 g) were extracted in Soxhlet extractors for six hours. After drying of the extracted residue (90°C) the change of sample dry weight was expressed as a percentage of petroleum ether soluble fractions (lipids). The percentage of volatile, petroleum ether soluble compounds was not determined. These volatile non-lipid compounds were assumed to represent a very minor fraction of the extract.

Analyses for protein, fibre and mineral nutrient content were made on dried material harvested on the slope of the IRB at the beginning, in the middle, and at the end of the 1970 growing season. Samples were analysed by the Soil and Feed Testing Laboratory of Alberta Department of Agriculture in Edmonton by using the standard analytical methods of the Association of Official Agricultural Chemists (1955). Quantitative determination of crude protein, crude fibre, calcium, potassium, sulphur, phosphorus and carotene was made on three species of vascular plants, detached roots, soil fibric organic matter and on the surface litter. The plant samples for analyses were prepared from a mixture of separated portions: photosynthetic (green) shoots, non-photosynthetic (brown) shoots, attached dead shoots and attached roots.

Results and Discussion

The results of lipid extractions of selected species are presented in Table 27. Lipid content of crest zone plants was in all cases higher than of that of plants growing in the transition. Both crest and transition plants show higher lipid levels than were found by Hubert (unpublished data) for the Truelove Lowland meadow species. Lipid content of beach ridge shrubs was higher than that of overgreen and deciduous alpine shrubs (2.93%) reported by Bliss (1962).

Raised beach sedges and herbs show also higher lipid content than alpine herbs (1.43%), (Bliss 1962b) and are comparable with lipid values of Pt. Barrow tundra graminoids presented by McCown and Tieszen (1972). These authors found surprisingly high lipid levels at the beginning of the growing season which indicates that

Table 27. Lipid content (%, n=2) of some selected species from the Intensive Raised Beach Site (IRB) July 7, 1970) and Plateau (August 1, 1970).

Species	Crest			Transition		
	Green	Brown	Roots	Green	Brown	Roots
Intensive Raised Beach Site:						
Dryas integrifolia	3.4	3.4	2.8	3.1	2.5	2.6
Salix arctica	4.1	5.6	5.9	4.0	4.5	5.5
Carex nardina	6.2	4.1	2.5			
Carex misandra	5.7	6.8	4.1	9.7	5.3	5.5
Saxifraga oppositifolia	5.7	6.8	4.1	3.0	3.9	3.3
Dead plants		1.0	1.0		1.0	1.0

	Total Shoots	Green	Brown	Roots
Plateau:				
Saxifraga oppositifolia	3.0	2.2	4.3	3.3
Cerastium alpinum	3.5			
Papaver radicatum	4.5			
Dead plants	1.0			

fatty compounds may play a significant role in metabolism of growing plants. At present there is, however, not enough evidence as to whether the accumulation of lipids at the beginning of the growing season is a consistent phenomenon.

In Table 28 analysed plants show very low phosphorus (*ca.* 0.08%) but high calcium (*ca.*2.0%) which gives unusually high Ca:P ratio (*ca.* 25:1). This is indeed of no surprise in a calcareous beach ridge substrate. In the Transition Zone, sedges and mosses occupied the site of an exposed old whale skull (Fig. 40), while in the Polar Desert near Resolute Bay (Cornwallis Island) *Saxifraga caespitosa* became established on a phosphorus richer old whale rib (Fig. 41).

Protein content (Table 28) was also low (*ca.* 6.0%) in the analysed plants. Levels of phosphorus and protein in beach ridge species are also lower than amounts of these compounds found in meadow sedges by Muc (1974). Striking are the relatively high amounts of crude protein compared to the protein content of plants in partially decomposed, detached roots, fibric organic matter and litter. This is probably due to the presence of soil microorganisms and invertebrates, especially *Nematodes*.

High content of crude fiber (*ca.* 50%) suggests the low digestibility of these plants except for their minute green parts.

There is no apparent difference in the protein, fiber, and calcium content in *Dryas* and *Saxifraga*. *Saxifraga* roots, however, show almost double the amount of phosphorus compared with *Dryas* roots. *Saxifraga* roots also show the highest caloric values of all species tested (see section Caloric Content). *Carex nardina* has

Table 28: Chemical composition and mineral nutrient content of plants, litter and soil organic matter on the slope of the IRB, 1970

Species	Plant part	Harv. #	Sample moist.	Crude protein (Nx6.25)	Crude fiber	Ca	P	Ca/P	K	S	Caroten mg/lb
			Percentage (air dry basis)								
Dryas integrifolia	Green	1	7.6	6.9	21.6	2.24	0.07	32.0	0.07	0.06	0.5
		3	5.3	7.4	30.4	1.75	0.11	15.9	0.25	0.06	2.1
		5	4.9	7.3	45.5	1.51	0.09	16.7	0.28	0.05	2.7
	Brown	1	8.1	5.9	13.4	1.84	0.07	26.3	0.11	0.07	0.5
		3	5.8	5.6	53.7	1.88	0.05	37.6	0.05	0.06	-
		5	5.4	5.6	58.3	1.53	0.06	25.5	0.12	0.05	-
	Roots	1	7.9	5.8	21.9	1.76	0.07	25.1	0.11	-	
		3	5.4	6.1	59.0	1.49	0.07	21.3	0.13	-	
		5	5.6	6.6	57.6	1.54	0.07	22.0	0.07	-	
	Stand. dead	1	8.5	5.3	55.8	2.20	0.07	31.4	0.07	-	
		3	6.4	6.3	52.9	2.33	0.06	38.8	0.08	-	
		5	6.3	6.4	54.0	2.14	0.06	35.6	0.06	-	
Saxifraga oppositifolia	Green	1	ND	5.0	ND	1.90	0.09	21.1	0.18	0.13	ND
		5	ND	ND	ND	1.43	0.10	14.3	0.31	0.13	ND
	Brown	1	10.2	6.8	15.4	2.48	0.08	31.0	0.10	0.11	
		3	5.6	5.0	55.2	2.62	0.08	32.7	0.10	0.13	
		5	5.9	5.0	51.8	2.46	0.07	35.1	0.10	0.10	
	Roots	1	6.9	6.2	21.9	2.08	0.13	16.0	0.13	-	
		3	6.5	6.6	55.3	2.06	0.11	18.7	0.12	-	
		5	4.0	6.3	53.0	1.78	0.11	16.2	0.14	-	
	Stand. dead	1	8.8	5.9	13.8	2.70	0.10	27.0	0.08	-	
		3	6.3	5.8	56.5	2.84	0.09	31.5	0.08	-	
		5	6.2	5.8	53.9	2.78	0.08	34.7	0.09	-	
Carex nardina	Green	1	ND	5.0	ND	1.90	0.09	21.1	0.18	0.13	ND
		3	ND	ND	ND	0.32	0.24	1.3	0.97	0.10	ND
		5	ND	ND	ND	0.60	0.10	6.0	0.26	0.06	ND
	Brown	3	ND	3.7	ND	0.47	0.05	9.4	0.18	0.06	
	Roots	1	ND	5.1	ND	0.96	0.09	16.6	0.16	-	
	Dead Plants	1	6.2	4.1	17.2	1.46	0.08	17.6	0.09	-	
		3	3.9	2.7	24.3	0.74	0.06	12.3	0.07	-	
		5	4.1	3.2	27.1	1.08	0.06	18.0	0.09	-	
Detached unidentified roots (0-10cm)		1	8.1	6.7	51.1	2.50	0.10	25.0	0.09	-	
		3	5.7	7.7	ND	2.41	0.09	26.7	0.07	-	
		5	5.3	7.2	ND	2.38	0.10	23.8	0.10	-	
Fibric organic matter (0-10 cm)		1	6.6	7.4	44.5	3.14	0.16	19.6	0.12	-	
		3	4.9	8.0	ND	3.40	0.16	21.2	0.12	-	
		5	4.8	9.7	ND	2.98	0.16	28.2	0.11	-	
Litter		3	5.7	7.8	ND	2.82	0.10	28.2	0.10	-	
		5	5.7	7.8	ND	3.32	0.09	35.8	0.12	-	

Harvest 1 (June 22)
3 (July 7)
5 (August 8)

ND - No data because of insufficient amount of sample material
- - traces only

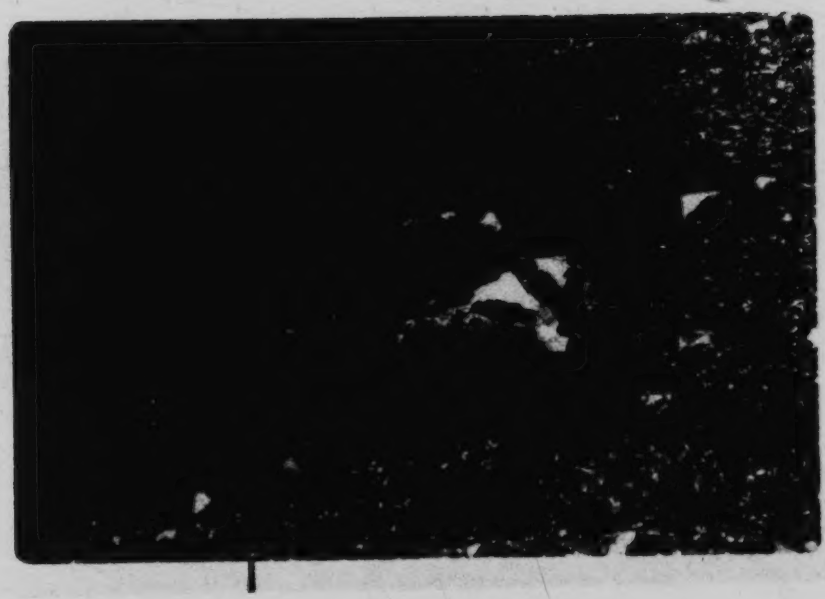


Figure 40. Buried old whale skull covered by lush vegetation. Raised beach in the Truelove Lowland, 1972.

Figure 41. *Saxifraga caespitosa* growing on an old whale rib bone near Resolute Bay, N.W.T. 1972.

much lower calcium levels than two other tested species, and its Ca:P ratio is therefore lower. Carotene content was determined only in *Dryas integrifolia* and is also very low.

Scotter (1972) presented data on the chemical composition of forage plants (*Salix glauca, Betula glandulosa, Ledum palustre, Arctagrostis latifolia,* and *Eriophorum vaginatum*) from the Reindeer Preserve near Inuvik, N.W.T. Only green leaves and twigs were analysed and they were not markedly different in crude protein and fibre content when compared with values of green leaves of the three beach ridge species. On the contrary, calcium content is much lower and phosphorus slightly higher in these low arctic species. Ratios of Ca:P are low and close to that found in *C. nardina.*

In a similar area Haag (1974) found 13.2% protein, 20.7% fibre and 0.27% phosphorus in *Betula nana* leaves, and 10.3% protein, 30.7% fibre and 0.13% phosphorus in the total material from the wet sedge meadow community near Tuktoyaktuk, N.W.T.

In an alpine environment on Mt. Washington the protein values for herbs and shrubs ranged from 15.3 - 20.8% and 10.3 - 14.9% respectively (Hadley and Bliss 1964).

Chepurko (1972) give 1.36% nitrogen (=8.5% protein) for leaves, 1.81% N (11.2% protein) for non-green shoots, and 1.11% N (6.9% protein) for roots of tundra dwarf shrubs in Khibini Mtn. (Kola Peninsula). In the same area alpine meadow shrubs had *ca.* 2.0% N (12.5% protein) in leaves, 0.90% N (5.6% protein) in non-green shoots and 1.6% N (10.1% protein) in roots.

Vascular species growing on elevated well-drained ridges with virtually no nutrient supply from the surrounding area may utilize

only these elements which may become available as a result of a direct weathering or as a result of direct deposition in faeces by animals. Levels of these nutrients in beach ridge soils are very low (see section on Soils, Tables 1 and 2). Meadow species on the contrary, which grow in depressions or flat basins, may have a certain advantage from the topographic situation and be supplied by nutrients produced elsewhere within a particular watershed. These limited data do not indicate any pronounced fluctuations of protein level as is discussed in Mooney and Billings (1962), Hadley and Bliss (1964) and Scotter (1972). They suggest, however, how limited the beach ridge environment is regarding some important nutrients. Moreover the physiological aridity (Sørenson 1941, Haag 1974) due to low soil temperatures may inhibit water uptake by the plants and consequently also cause both limited nutrient supply and their uptake by plants.

Caloric content

Methods

Caloric content was determined from the dry material harvested in 1970. Fine ground plant parts (20 mesh) were pellatized and combusted in an Automatic 1200 Adiabatic Oxygen Bomb Calorimeter (Parr Instrument Co. Inc.). Caloric values of cushion species from the beach ridge were determined for the total shoot as well as for separated plant parts: live green, live brown, standing dead and roots.

Results and Discussion

Analysis of the results (Table 29) leads to the following conclusions :

a) the caloric values of Polar Semi-desert "evergreen" shrubs (*Dryas integrifolia* - 5259 cal . g^{-1}, and *Cassiope tetragona* - 5816 cal . g^{-1}) are markedly higher than evergreen alpine tundra shrubs (5098 cal . g^{-1}). Values for beach ridge *Saxifraga oppositifolia, Carex misandra* and *C. nardina* are also higher than average figures for alpine tundra herbs (4601 cal . g^{-1}) found by Bliss (1962).

b) roots of *D. integrifolia* and *C. tetragona* show a decline in caloric value at the beginning of the growing season.

c) live brown shoots of all species tested had higher caloric content than green shoots and leaves. The degree of lignification is probably responsible for higher caloric values of woody shrubs, and brown parts of herbs.

d) roots of *Saxifraga oppositifolia* show record ash-free caloric values (over 6000 cal) for which I lack the explanation. Even higher values (7000 cal) were found by Zachhuber (1973, personal communication) in roots of *S. oppositifolia* growing at high elevations in the Austrian Alps.

e) Mean ash content in shrubs ranged from 3% (green parts) to 6.5% (standing dead), in sedges 3.6% (green parts) to 6.5% (roots), and in *Saxifraga oppositifolia* which represents a cushion herb, values ranged from 5.9% (green) to 13.4% (standing dead). Ash content of herbs growing on the plateau was lower, *ca.* 1.5% on average.

Determination of caloric values in plants has a merit in

Table 29. Caloric content of species collected in 1970 (cal . g^{-1} dry weight ± 1.5%).

Species and Harvest	St. dead	Roots	Live brown	Live green	Total shoots
SHRUBS:					
Dryas integrifolia - raised beach ridge					
1.*	5155	4805	5291	4950	4342
2.	4959	5085	5194	5110	5252
3.	4989	5310	5305	5164	5164
4.	5007	5393	5263	5088	5222
5.	5004	5252	5242	5159	5186
Mean values	5022 (4530)	5169 (4930)	5259 (4978)	5094 (4824)	5003 (4876)
Cassiope tetragona - raised beach ridge					
1.	5727	4466	5743	5616	5823
2.	5720	5270	5797	5673	5883
3.	5620	5448	5774	5737	5491
4.	5503	5238	5900	5586	5565
5.	5678	5365	5867	5716	5741
Mean values	5650 (5396)	5157 (5053)	5816 (5670)	5665 (5538)	5701 (5508)
Salix arctica - raised beach ridge					
1.		5176	5377	5014	
2.		5296	5347	4870	
3.	5169	4891	5340	5003	
4.		5170	5284	4956	
5.	5258	5222	5239	4772	
Mean values	5214 (4925)	5151 (4951)	5317 (5057)	4923 (4826)	
Mean values for shrubs:					
	5294 (4950)	5159 (4977)	5464 (5235)	5227 (5062)	5351 (5191)

Table 29 (cont'd)

GRAMINOIDS:	St. Dead	Roots	Live brown	Live green	Total shoots
Carex nardina -raised beach ridge					
1.		4935	4734	4657	4570
2.		4630	4700	4600	4807
3.	4647	4805	4784	4740	4678
4.		4858	4735	4674	4763
5.		4917	4737	4650	4837
Mean values	4647 (4364)	4829 (4178)	4738 (4300)	4664 (4468)	4731 (4286)
Carex misandra - raised beach ridge					
1.	4522	4724			4780
2.		4577	4701	4540	4429
3.	4712	4964			4697
4.		4672	4681	4663	4671
5.		4703			4612
Mean values	4617 (4496)	4728 (4505)	4691 (4485)	4602 (4466)	4638 (4523)
Carex rupestris - raised beach ridge					
3.					4660
5.	4581	4558			4652
Mean values	4581(4550)	4558 (4520)			4656 (4632)
Mean values for graminoids:	4615 (4469)	4705 (4400)	4714 (4392)	4632 (4467)	4674 (4479)
HERBS:					
Saxifraga oppositifolia -raised beach ridge					
1.	4673	6121	4786	4686	4665
2.	4837	5513	4930	4707	4911
3.	5077	6055	4973	4702	4996
4.	5121	5755	4726	4680	4823
5	5665	6482	4823	4655	4905
Mean values	4955 (4292)	5985 (5519)	4828 (4353)	4686 (4408)	4840 (4477)

Table 29 (cont'd)	Roots	Total Shoots
Saxifraga caespitosa - Plateau		
	4006 (3960)	3204 (3165)
Saxifraga nivalis - Plateau		
	4533 (4454)	3737 (3668)
Arenaria rubella - raised beach ridge		
		4121 (4073)
Draba alpina - raised beach ridge		
		4602 (4595)
Oxyria digyna -raised beach ridge		
	4482 (4335)	4238 (4189)
Papaver radicatum - Plateau		
	4694 (4663)	
Pedicularis lanata - raised beach ridge		
	5014 (5013)	4592 (4580)
Polygonum viviparum - raised beach ridge		
	4902 (4072)	4150 (4106)
Silene acaulis - raised beach ridge		
	4516 (4499)	3793 (3612)
Mean values for herbs:		
	48.7 (4687)	4333 (4232)
Unidentified Roots - raised beach ridge		
0-10 cm	4920 (3982)	
10-20 cm	5019 (4258)	
MOSS - raised beach ridge		4644 (4075)
LICHENS - rock outcrop		
Thamnolia vermiculata		4480 (4264)
Cetraria cuculata		4290 (4036)
Umbelicaria lyngei		4400 (4335)
LITTER - raised beach ridge		4911 (4448)

*Dates of harvests: (1) June 22, (2) June 29, (3) July 7, (4) July 20, (5) August 5. Numbers in parentheses represent the original caloric value, i.e. with ash. All other figures are ash-free values.

ecological and energy budget studies as was shown by Long (1934), Golley (1961), Bliss (1962), Hadley and Bliss (1964) and others.

Very little or no significant change is usually found in caloric values in relation to the fluctuation in carbohydrate content. Rochow (1969) studied *Caltha leptosepala* in relation to snowmelt. In plants which were released early from a snowbank, caloric content decreased over the season while total sugars showed constantly high levels. Caloric content of plants from a late snowbank increased during the season while total sugars remained at a low level. There is a reasonable conjecture that the fluctuation of caloric values during the season may be influenced by the building and breakdown of hemicelluloses (McCarthy 1938, Roshchevskaia and Schvetsova 1970).

A comparison of the mean caloric values of *Salix* species collected in three environments supports the assumption that the caloric content of woody plants is positively correlated with the degree of environmental stress :

Species	cal . g^{-1} ash-free dwt.	Site
Salix herbacea	4969	Mt. Washington, New Hampshire. Bliss 1962b.
Salix uva-ursi	4879	
Salix planifolia	4866	
Salix arctica	5106	Hummocky sedge meadow Muc 1972
Salix arctica	5317	Slope, Intensive Raised Beach Svoboda (Table 29)

Woody plants have generally higher caloric content than herbs as was documented by Bliss (1962b), although the exact amount varies among species and region.

Dryas integrifolia: A Dominant Cushion Species on Raised Beaches

Dryas clumps as a micro-ecosystem

The information on *Dryas* phenology, growth, productivity energy and nutrient content is presented in previous chapters.

Porsild (1964) characterized *Dryas integrifolia* as "an ubiquitous pioneer species on frost heaved, calcareous, gravelly and rocky barrens and in the western islands probably the most common and widespread phanerogam".

Not much has been done on *Dryas* autoecology aside from the Devon Island Project and this chapter should not substitute for such a study. It contains, however, information put together with the intention of using *Dryas* as a representative "pars pro toto" species of the raised beach community.

Dryas integrifolia was chosen for modelling purposes by Whitfield (1973) because its clumps behave like a micro-ecosystem where the growth and decaying processes occur *in situ*, where microflora and microfauna increase with the growing and expanding clump, and where soil forming processes occur much more under the clump than between clumps. In this respect, a *Dryas* plant appears to be a semi-closed system, which absorbs nutrients as they are available from the very limited surrounding sources. It holds and most probably recycles some of these nutrients as released in decomposition.

Dryas integrifolia is the most characteristic species of the Polar Semi-desert community, but there are almost barren ridges in other Devon Island lowlands (e.g. Sparbo Hardy Lowland) where *Dryas* is only a minor component or is absent completely. This is probably

due to some edaphic factors (*Dryas* is a calcareous soil loving plant), or is due to sites notably exposed to winds.

In the Truelove Lowland raised beach complex, *Dryas* is the dominant species. It comprises 47.5% of the Crest, 77.7% of the Slope and 70.5% of the Transition Zone standing crop on the IRB.

Dryas seedling establishment is a rare event, not completely understood yet. Very few small *Dryas* plants have been found and even these are usually more than twenty years old. There is a high probability that new plant establishment occurs within old clumps, as was observed by the author in *Saxifraga*. A seed germinates and a new seedling gets established in an already existing mat of a partially dead plant clump. There is also a certain potential for vegetative reproduction of mechanically destroyed plants. Two or more new clumps can develop as a result of an old clump that disintegrates in the centre.

A *Dryas* clump is green only on the surface. Old leaves which finally die remain attached and after years they become part of the clump core and decay *in situ*. Nutrients released are leached down to lower strata and may be absorbed again by fine roots which develop in the decomposed and humified organic matter above the surrounding ground surface. We believe that this process also operates in other cushion species of the High Arctic which slowly accumulate the necessary nutrients for growth, and create from a sterile and purely mineral environment, a bioenvironment.

An attempt to schematize the plant-soil decomposition system represented by a *Dryas* cushion is shown in Figure 42. Microflora and microfauna, present in and on dead but still structured old

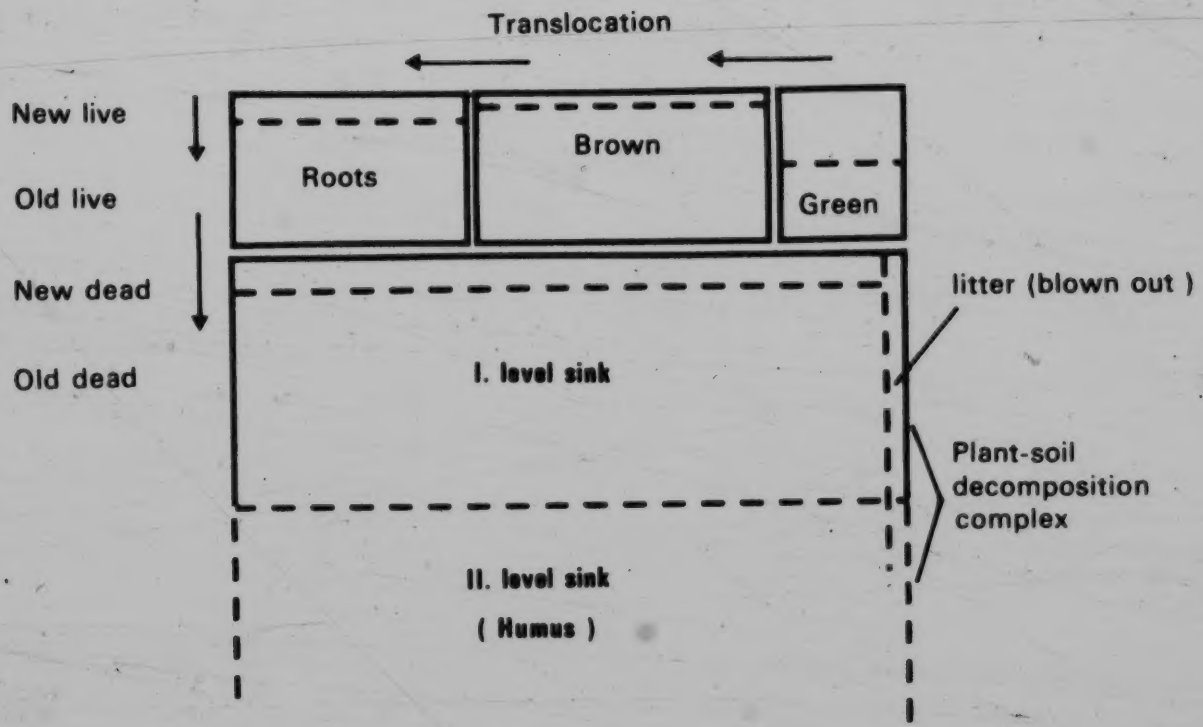


Figure 42. Diagram of biomass distribution in a *Dryas* cushion.

plant parts, mainly leaves, are the first level energy sink. The second level sink represents the humified material, where the remaining energy is stored.

There is a gradual transition between the structured and totally humified organic matter in the cushion. Figure 43 shows the distinct vertical stratification within a *Dryas* clump. One can distinguish several differently colored layers of dead leaves. These layers or strata are of increasing age and an analysis of their carbonydrate and caloric content shows significant changes over time (Fig. 45). The uppermost layer is formed by green leaves which live for two seasons. The dying leaves become yellowish brown and form a thin second layer. Leaves remain in this condition 3-5 years before they turn gray. The gray layer is usually thick and 5-20 years old. The completely leached and carbonified leaves form a black layer of undetermined age. The last two are the black disintegrated and the dark brown humified layers. Based upon mean shoot increment per year and mean shoot legnths, many clumps are 80 to 120 years old.

All parameters measured showed decreasing values with age and indicate the rate of decomposition and energy losses from the core of the clump. The most dramatic shift is the loss of carbohydrate from leaves as they die. Leaf weight and caloric changes are much slower (Fig. 45).

The organic matter has also its microclimatic significance. It works like a sponge which absorbs and holds water long after the surrounding area dries out. It also buffers the fluctuation of temperature, mainly by reducing daily maxima.

All biomass which was formed during the life of the plant is

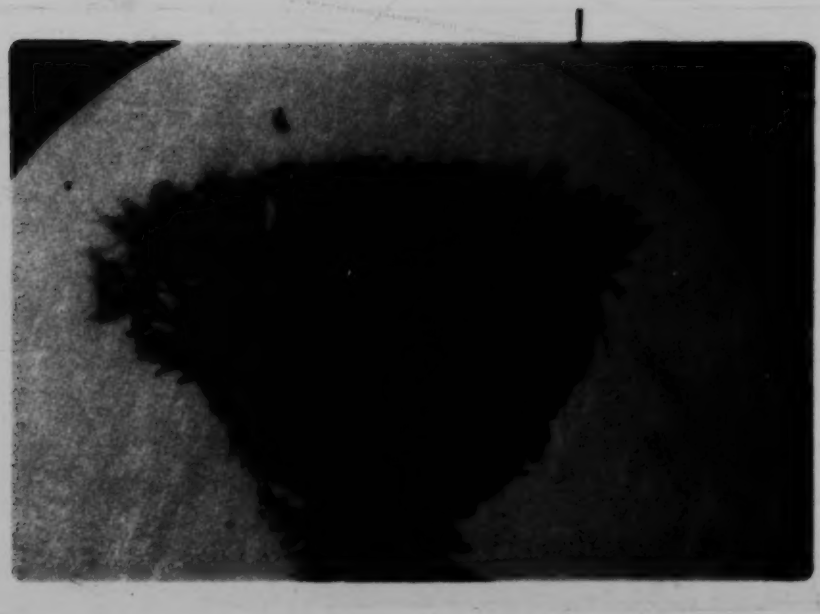


Figure 43. Vertical stratification within a *Dryas* clump.

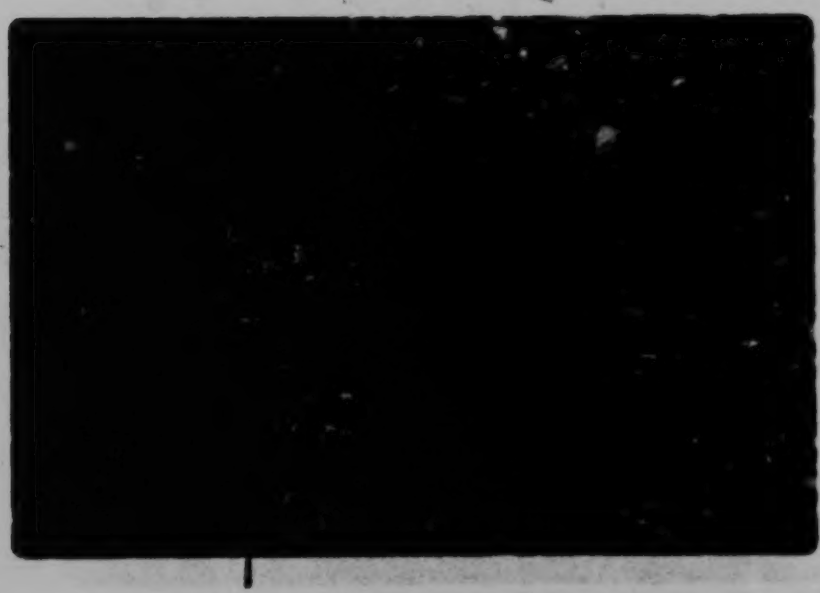


Figure 44. Sicle shaped *Dryas* clump growing on an exposed ridge with prevailing NW winds. 1972.

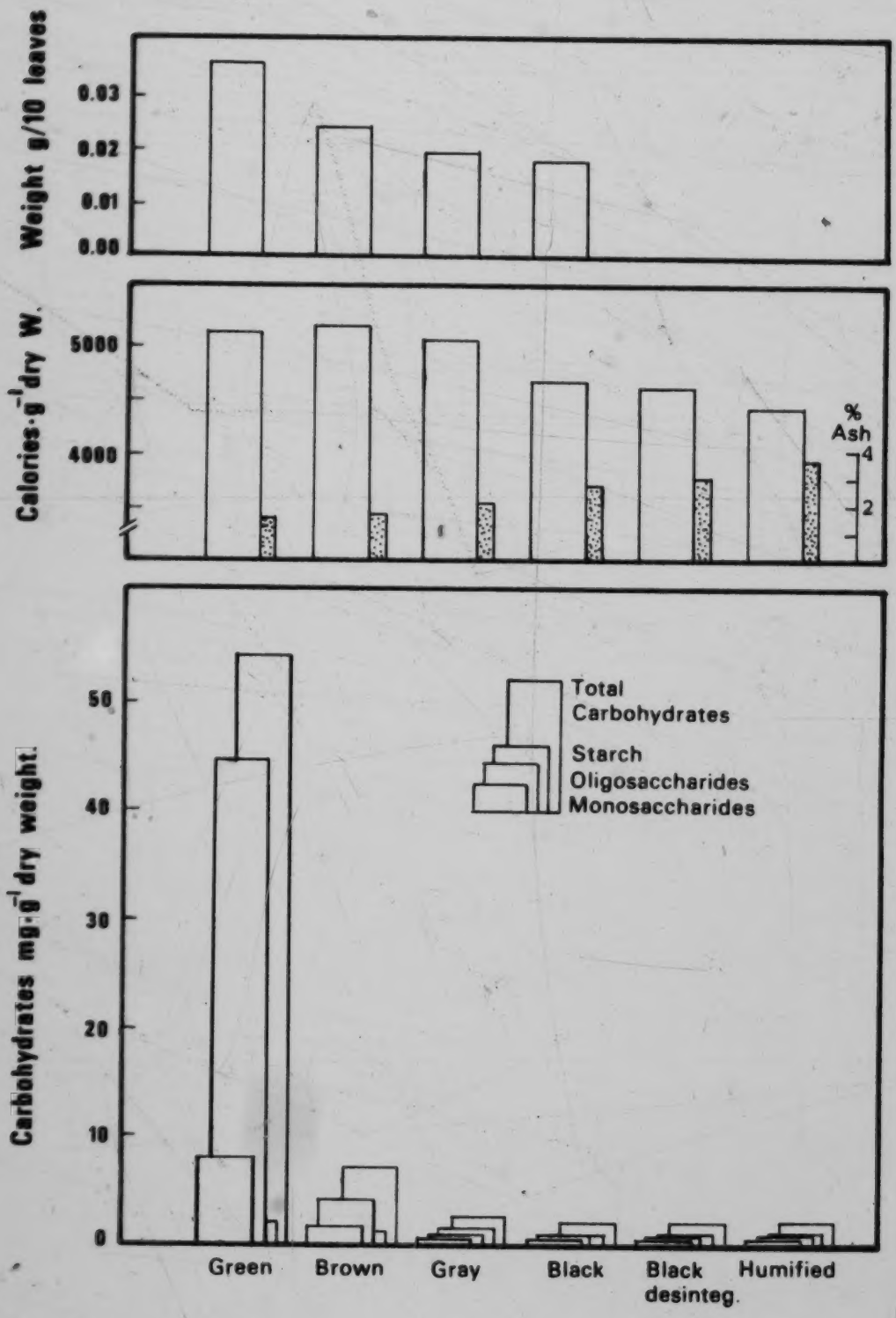


Figure 45. Analysis of various strata in the *Dryas integrifolia* cushion, IRB, August 17, 1972.

still present as an incorporated standing dead. The non-combustible (ash) content increases in older strata. All these suggest that the plant can, at least partially, make use of the products of disintegration of its own parts as indeed any closed stand of vegetation does.

Asymetric growth of *Dryas* clump and its leaf angle orientation

Leaf canopy and architecture in relation to light penetration and photosynthesis has been studied by Warren Wilson (1965), Philip (1965), Pearce *et. al.*, (1967), Kuroiva (1969), Douglas and Ramsden (1973), and special devices for leaf angle measurements have been constructed by Kvet *et al.*, (1967), Whitfield and Svoboda (1974), and others.

Methods

Leaf angle measurements on *Dryas integrifolia* clumps were made with a special device designed by Whitfield and Svoboda (Fig. 46). A plastic protractor was loosely hinged to the pointer manipulated by the researcher in the direction of leaf growth. The leaf angle orientation to the horizontal plane can be read directly on the protractor. The compass orientation of the leaf is pointed by the handle of the device and read on the "clock" established around the clump (Fig. 47). The compass orientation was recorded in 12 classes (i.e. 12 hours; 30° per class). The 12th hour represents North.

Each *Dryas* plant was divided into four 90° compass segments. A total of 150 leaves were randomly measured in each segment and recorded. Slope orientation, size and height of the clump were also

Figure 46. Leaf angle device designed for measurement of very small leaves.

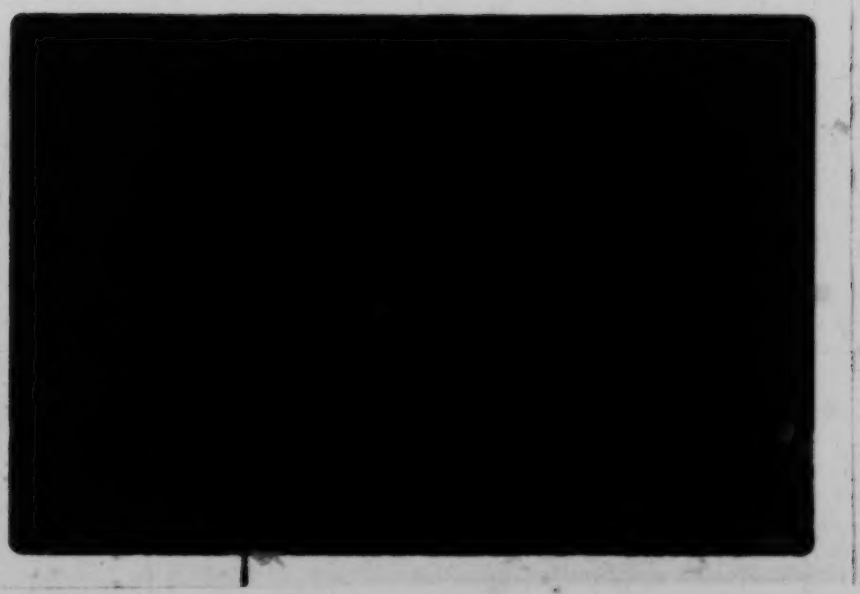


Figure 47. Leaf angle measurement on a *Dryas* cushion.

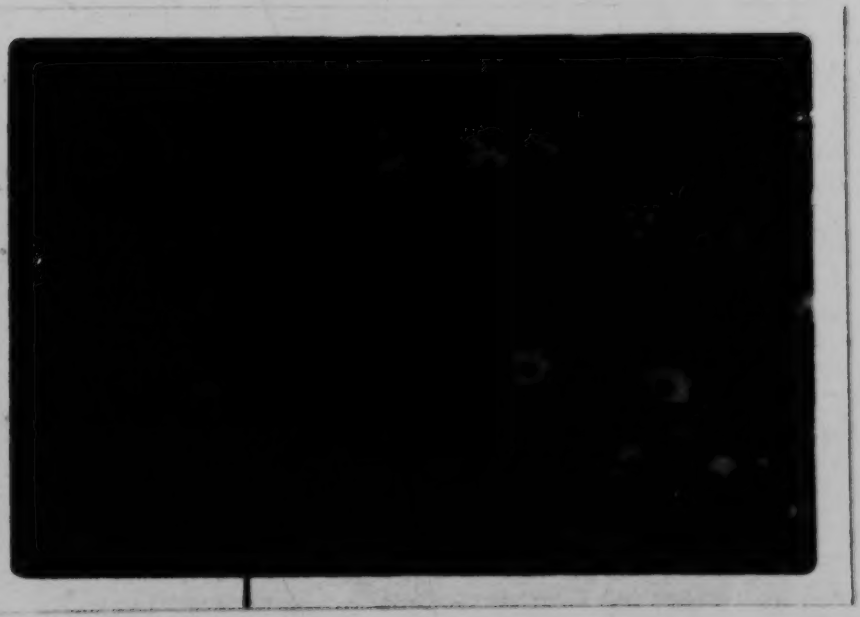


Figure 48. Hemispherical *Dryas* cushion growing on a barren rock in the Truelove Lowland 1972.

recorded for eventual correction of the obtained data. Leaf angle measurements were conducted in two plants growing on the crest and on one plant in the transition of the IRB.

Results

Wind velocity increases above the ground surface. This and the lack of deep snow cover during winter confine arctic plants to a very shallow spatial niche and keep them low in growth form. Even in this profile there are noticeable differences in wind speed between the windward side and lee side to which the plant is sensitive and reacts by its growing in a leeward direction (Fig. 44 and 49).

Measurements on three large plants supplied the following information on the uneveness of *Dryas* clump growth. The clumps were divided into four compass segments, each segment with an assumed theoretical chance to be covered fully (i.e. 100%) by green leaves. The actual green leaf coverage was far below the theoretical expectation, and was different in each compass segment (Table 30).

Table 30. Percentage of segment area covered by green leaves.

	Raised Beach Zone					
	Crest		Transition			Mean of
Segment	Plant 1	Plant 2	Plant 3	Mean		two segments
North	84	71	26	60.3	NW	70.3
East	91	71	92	84.6	NE	72.4
South	87	85	97	89.6	SW	84.6
West	85	83	73	80.3	SE	87.1

Leaf and shoot samples collected from these four compass

segments of the plant measured for leaf angles in the Transition Zone show (Table 31) leaf length and weight were higher on the exposures, favoring higher temperature and perhaps light.

The growth form of an ideal *Dryas* clump is hemispherical (Fig. 48). In reality, only clumps on soil hummocks, rock outcrops and some in the mesic Transition Zone achieve this growth form, sites that have adequate winter snow cover and protection from winds. *Dryas* clumps on the crest and slope are flat (Fig. 22). For *Dryas* the chance to survive is associated with the possibility to form a cushion. *Dryas* clumps show a considerable variation in cushion shape, growth rate, leaf size, green leaf cover per unit area of clump, and leaf angle orientation. On exposed localities, clump growth follows the predominant air streaming near the ground and this may be different within a small area. Figure 44 shows a sickle shaped *Dryas* clump found on Rocky Point where the cold NW wind from the frozen ocean still prevails in July. All clumps grow in a SE direction here and die on the opposite side. Figure 49 was redrawn after Warren Wilson (1959) in order to demonstrate the effect of wind on the plant clump.

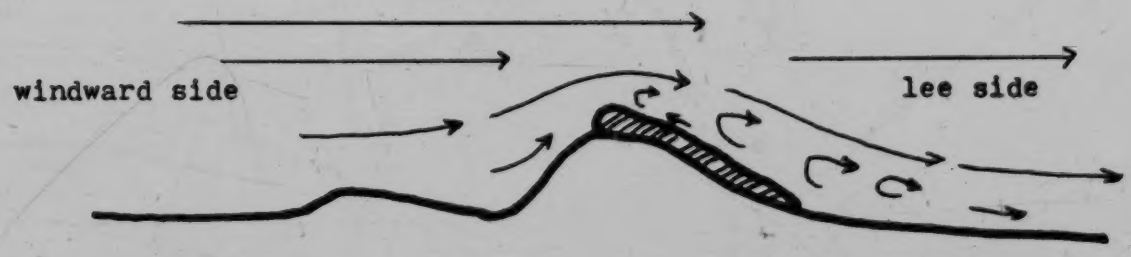


Figure 49. The wind speed near the ground and around an exposed plant clump. Redrawn after Warren Wilson (1955).

Table 31. Mean length (mm) and mean dry weight (g) of one green *Dryas* leaf according to its position on a shoot in different compass segments of a clump. Each number is a mean of 15 measurements.

Segment	Sequence of leaves on a shoot 1	2	3	4-6	Total green shoot
Length (mm)					
North	4.4	7.3	9.1	10.5	
East	6.6	12.7	12.3	15.7	
South	6.6	13.4	14.6	16.7	
West	5.8	10.8	12.0	15.2	
Dryweight (g)					
North	.0018	.0052	.0071	.0104	.01253
East	.0026	.0087	.0086	.0138	.01425
South	.0033	.0096	.0119	.0169	.01776
West	.0033	.0072	.0106	.0174	.01503

In this study information about leaf canopy and leaf angle orientation was gathered in order to explain whether a *Dryas* cushion operates as a simple hemispherical surface with its small leaves distributed randomly, or whether leaf orientation is non-random. By changing leaf angles the platn would control the exposure of its foliage to direct radiation.

One big hemispherical *Dryas* cushion was measured in the Transition Zone and two other flat *Dryas* plants were chosen in the Crest Zone (Table 32).

Table 32. Growth parameters of three *Dryas* cushions from IRB

Parameter	Crest		Transition
	Plant 1	Plant 2	Plant 3
Length x width x height (mm)	440x250x40	430x270x35	500x360x140
Predominant clump orientation	NW-SE	NE-SW	N-S
Total area of clump (cm^2)	850	1166	1413
Covered by green leaves (cm^2)	740 (87%)	902 (77%)	1049 (74%)
Percentage of green cover in each segment, and from the total area ()	N 84 (21) S 87 (22) E 91 (23) W 85 (21)	N 71 (18) S 85 (21) E 72 (18) W 84 (21)	N 26 (7) S 97 (24) E 92 (23) W 73 (18)

Figure 50 represents a graphic illustration of leaf angle orientation in four compass segments on a hemispherical *Dryas* clump from the Transition Zone. The majority of leaves grow in a radial

direction in all segments. The size of individual leaves and their total cover is different in each segment (Table 30).

Although leaf angle orientation visually appeared to be almost random, the measurements show that most of the leaves which grow in the clump are oriented in the range from 10 to 30° to the horizontal plane. Leaf azimuth orientation was strongly influenced by the compass orientation of the particular segment. In other words: new shoots grow in the direction of an available space but at different rates in each compass segment.

Two other clumps were measured on the crest of the IRB. These clumps were flat and only 35-40 mm high. Figure 51 shows that leaf angle orientation is more evenly patterned and that polarization to margins is less pronounced compared to the *Dryas* clump growing in the Transition Zone. There is a slight tendency of leaf azimuth orientation in a direction to the open space. The dominating leaf angle orientation to the horizontal plane is 30 to 50° in all segments.

Discussion

Results of *Dryas* leaf angle measurements lead to the following conclusions:

a) majority of leaves are oriented in an angle range which is close to the range of the noon sun's angle of incidence in summer for this latitude (37°31' above the horizon at noon June 21). Such an orientation may substantially lower the direct exposure of sun-facing leaves to the sun rays, and on the other hand it may slightly increase the illumination of sun deflected leaves. On a hemispherical surface, leaves on the sun deflected side will shade each other more than on

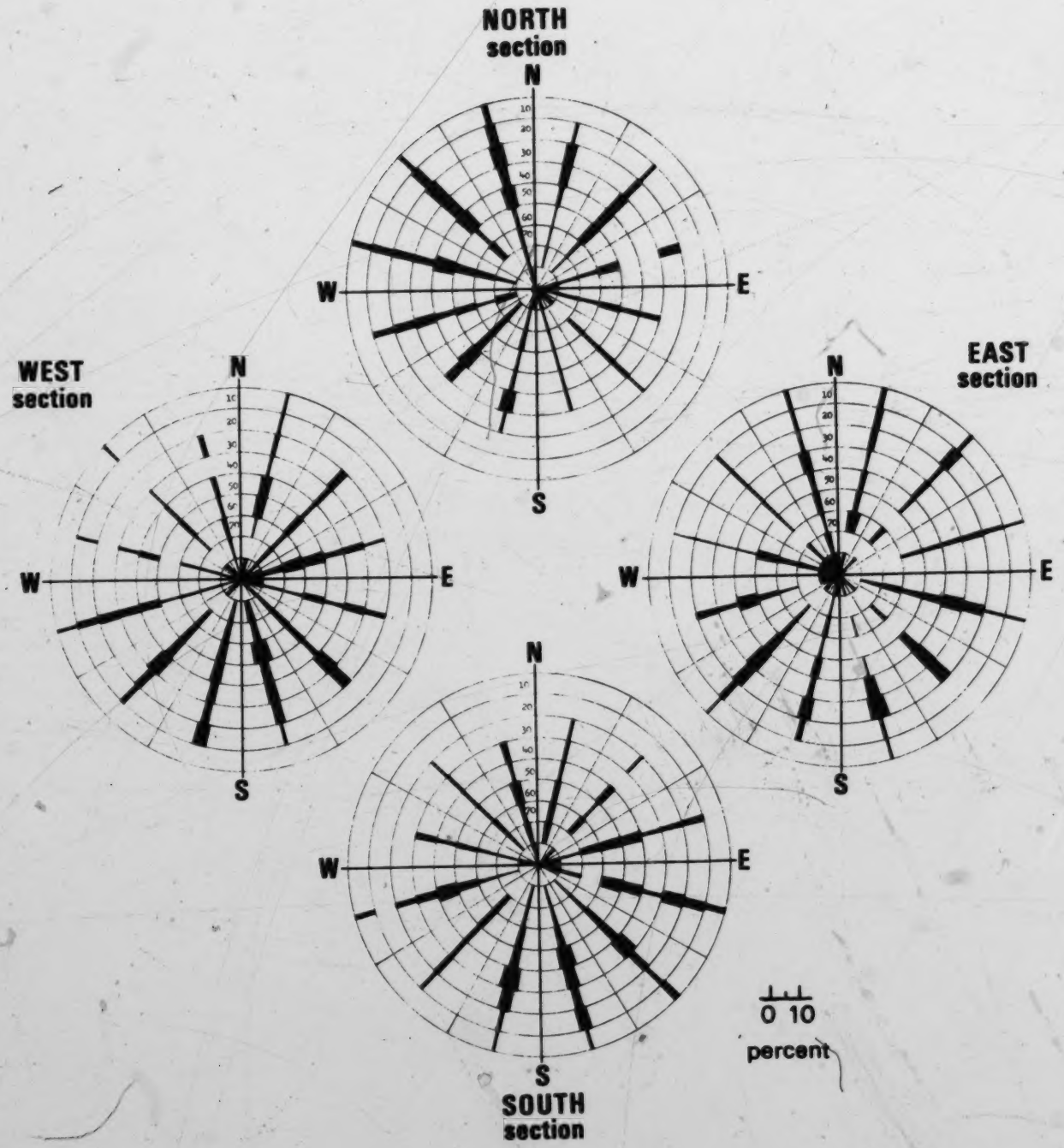


Figure 50. Leaf distribution and leaf angle orientation for a *Dryas integrifolia* clump, Crest Zone, 1972.

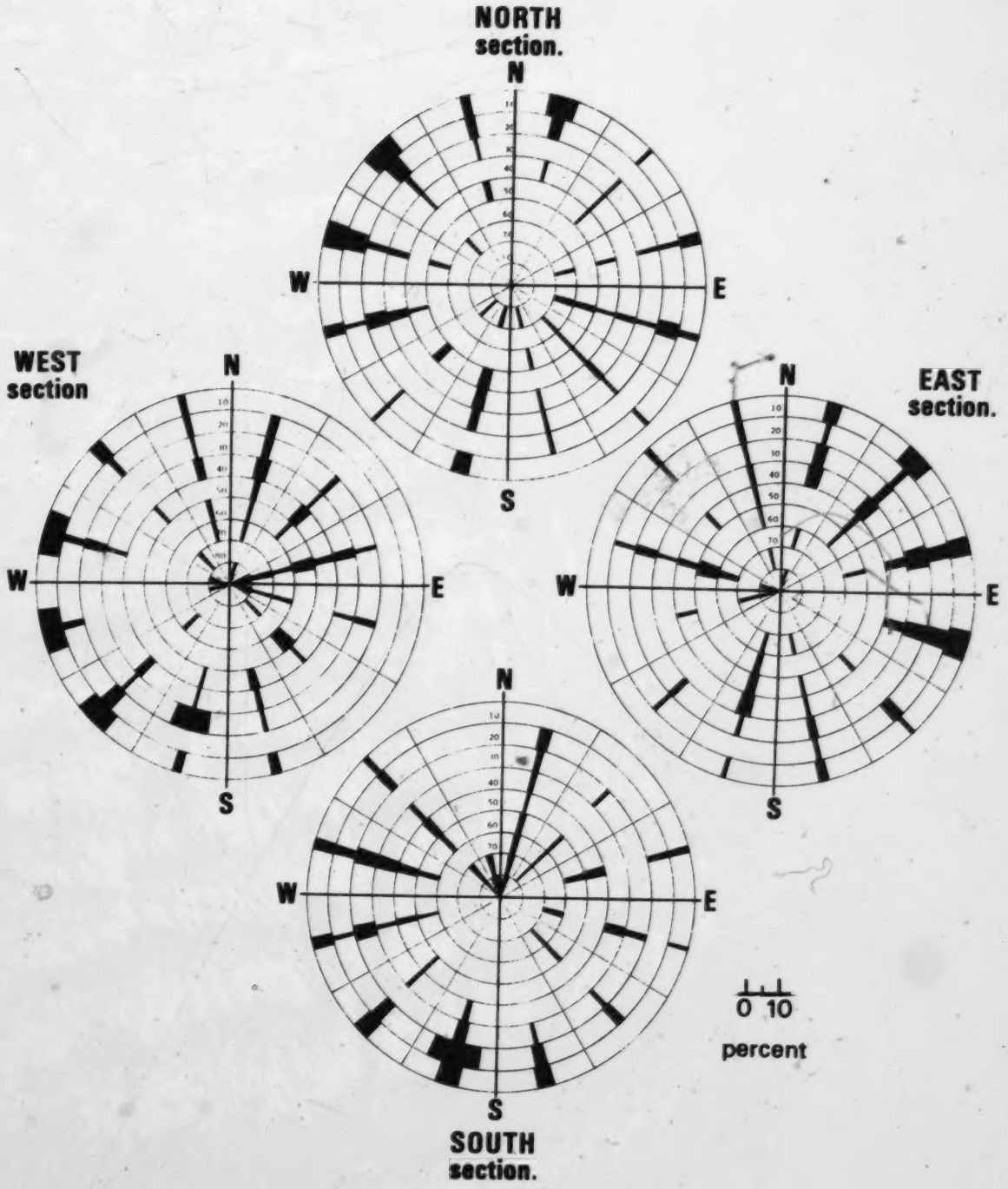


Figure 51. Leaf distribution and leaf angle orientation for a *Dryas integrifolia* clump, Transition Zone, 1972.

the sun facing side and thus they may tolerate higher illumination (Fig. 52).

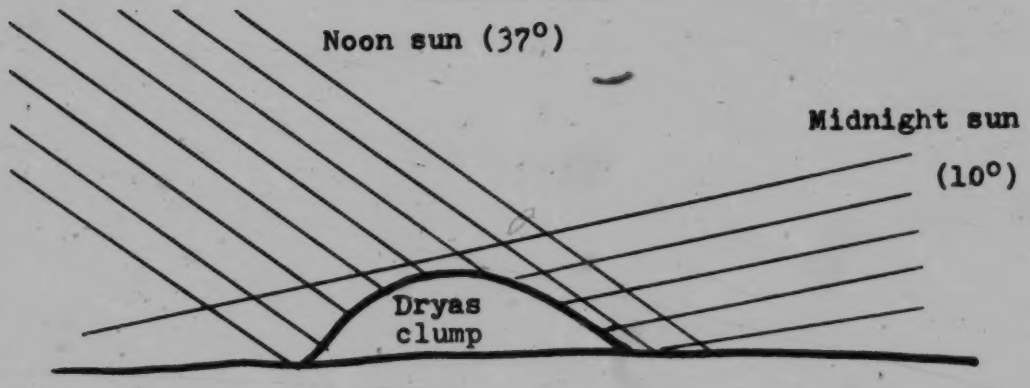


Figure 52. The angle of sun rays incidence during noon and midnight on June 21 in relation to the horizontal plane and a hemispherical *Dryas* clump.

b) this apparent strategy seems to be in agreement with a low light compensation point and with an optimum rate of net photosynthesis during the "night" and on cloudy days (Mayo *et al.*, 1973). The direct and full exposure of *Dryas* leaves would lead to a potential intolerable rise in leaf temperature and therefore to high respiration rates. On the Truelove Lowland, "nights" and cloudy days dominate over sunny days during the growing season.

The 10 to 30° leaf arrangement in the Transition Zone and 30 to 50° leaf orientation on crest zone clumps can therefore be interpreted as a negatively sun oriented or a positely sky oriented arrangement, an adaptation which enables the plants to minimize leaf

exposure to the direct "hot" sun beam and to retain exposure to a "cool" diffuse light.

Viereck (1966) and Lawrence *et al.*, (1967) stress the role of *Dryas drumondii* and *D. integrifolia* in the initial invasion and pioneer stage of the gravel outwash vegetation in recently deglaciated areas in Alaska. They rapidly stabilize the ground surface and enable the invasion of other dependent species. The soil undergoes rapid changes due to organic matter accumulation and nitrogen fixation via nodulated *Dryas* roots is considerable. *Dryas* speeds up the rate of succession in these areas by a period of 20-30 years.

In the Truelove Lowland, *Dryas* is not a nitrogen fixer (Stutz 1973), its role in humification, however, is important because it creates a favorable microclimate for the nitrogen fixing bacteria.

Aleksandrova (1970a) and Tieszen (1972) emphasize the importance of litter accumulation under the cushion of arctic plants. It protects the basal meristems and enables young shoots of some species to start photosynthesis shortly after snowmelt. In summary it is possible to state that *D. integrifolia* is a representative species of the Polar Semi-desert community which is characterized by an unusual growth form and strategy. It is able to occupy sites with low available soil moisture and nutrients and with relatively high soil surface temperatures. It maintains a large aboveground biomass in which the standing dead seems to be highly functional as a microclimatic agent and supplementary nutrient pool. It has a small but long-living root system and small photosynthetic surface with leaves designed to live for two seasons. These adaptations enable *Dryas* to grow in sterile calcareous substrates that are relatively dry and warm. There

is little if any indication that other species are better adapted to replace it over time. Therefore, it does not play the role of a successional species in the High Arctic as it may do in southern arctic and alpine environments.

SYNTHESIS

Raised beaches have been convenient for community and production studies within the Arctic for three main reasons. They exist as distinct landforms of similar and easily defined structure, their age can be determined, they contain zonal soil Arctic Brunisol (Arctic Brown), and they play a key role in the biological functioning of several of these high arctic ecosystems. In Truelove Lowland almost every raised beach indcludes a vegetational continuum starting with a more densely inhabited transitional zone and ending often in barren Polar Desert-like crests.

Regarding methods used in this study there are technical problems, not yet completely solved, concerning production estimates of perennial dwarf shrubs. Extremely low annual growth of *Dryas integrifolia*, *Saxifraga oppositifolia* and other species, and their heterogenous distribution make the usual method of regular quantitative harvesting per unit area of little use (Andreev *et al.*, 1972) unless this method is complemented with the production estimates from individual species.

Warmer temperature near the ground confines shoots and roots of these plants to a very narrow spatial niche, denying them the possibility to extend in both vertical directions. Near the ground, these plants experience high temperatures during sunny days which often imposes other stresses on them because this stimulates their water demand and increases respiratory rates. In dry habitats, due to low availability of water and associated low availability of nutrients, xeromorphic characters develop, demonstrated by low protein and high fibre contents, and thickening of the cuticle as

found in the Low Arctic (Haag 1972).

On raised beaches the phenological pattern of *Dryas* sets the overall community production pattern because this is the dominant species, 48% by cover and 75% by biomass. It was for these reasons that *Dryas integrifolia* was chosen as representative of high arctic cushion species for further intensive study.

The cushion community (except for a few non-cushion species) does not produce free litter. Dead organs (also leaves) stay attached to the stems for many years and even decades. This results in a special ability of a cushion plant to protect its growing points (Savile 1972) and to improve greatly the microclimate inside the clump with respect to higher temperature, moisture, microbial activity and mineral recycling in a semi-closed system. Although there is almost no litter accumulation on the surface of the ridge, the A- horizon contains more organic matter than we can reasonably expect in relation to the aboveground biomass. For example, Shamurin's (1972) data from Tareya spotted *Dryas*-sedge-mossy tundra shows the vascular plant root:shoot ratio of 17.6:1 and those from apparently dryer hummocky *Dryas*-sedge-mossy tundra, a root:shoot ratio of 36.7:1. It is hard to believe that 1 unit of live aboveground biomass can nourish 17 to 36 units of underground organs, especially when the photosynthetic:non-photosynthetic ratio is low. It is apparent that most of the underground biomass is dead (as are most of the shoots). Because of extremely low decomposition rates it is accumulating as "underground litter".

Species diversity, cover, standing crop and production values are low to very low on raised beaches. The efficiency of incoming solar

energy utilization is only 0.3-0.4% in July and only 0.1% in early August. Carbohydrate reserves (1-5%) as well as protein (5-6%) and nutrient contents are very inadequate even when compared with plants from less unfavorable arctic habitats. All these features of these cushion plants make detailed ecophysiological and genetic studies of great importance if we are to understand how these species are adapted to these extreme polar environments.

In comparison with alpine environments where plant life is strongly controlled by high fluctuations in temperature (Bliss 1971) and for example with Irish blanket bogs which are generally nutrient limited (Moore 1970), the high arctic environment is both temperature and nutrient limited. Polar Deserts and Semi-deserts are also moisture limited systems. Polar desert plants live in conditions which seem to be far below their optimum. This follows from the greenhouse and fertilizer experiments (see p. 176) and from the comparison with individuals of the same species growing in a more favorable Polar Semi-desert habitat. This introduced questions about their survival potential, degree of adaptation, and ways of reestablishing plants in a quasi-succession.

It seems that some populations which grow in extreme polar habitats where they are exposed to most vigorous environmental stresses are not fully selfsustaining. They very probably depend on a resupply and reinforcement by seed from plants growing in more favorable habitats, sometimes quite remote. These exposed plants can be viewed as species "messengers" pioneering in areas where the species cannot fully survive on its own.

These "marginal" populations whose individuals are "relatively sparsely distributed and show effects of physiological stress"

(Soule 1973) are closest to extinction but may also be considered the most resourceful breeding material for more resistant new strains if they are able to produce viable seed.

The cushion plant community type decreases in species diversity going from rock outcrop sheltered sites and the Transition Zone of raised beaches to their slope, crest and finally to the outer edge of the plateau. Most of the small herbs which accompany the dominant species in the most favorable sites are already rare on crests, but do not disappear completely on plateau. Hutchinson (1959) postulates that "in areas where the fundamental productivity is limited by short growing season the rare species in a community may become so rare that they do not exist". Although Hutchinson's statement treats rare species merely as a statistical event of certain probability (there is no direct causality between low community productivity and absence of rare species) its predictive value is high and can be validly applied to the whole raised beach gradient except for the plateau. Here *Dryas* and *Salix* are present only along the plateau edge and the forbs, *Papaver radicatum, Cerastium alpinum, Saxifraga oppositifolia* and few othrs continue to the very edge of the ice cap.

Margalef (1963, 1969) suggested the productivity:biomass ratios as an "inverse" index of diversity. Under non-limiting conditions simple ecosystems such as starting successions or man regulated crop fields are the most productive, so that the inverse correlation between production per unit biomass and community diversity is very close. In the Truelove Lowland Margalef's theory can be reasonably applied to meadows, rock outcrops and raised beach transitions. Meadows are low in species diversity but much higher in production

than rock outcrops and transitions with higher species diversity.

Polar deserts and Semi-deserts, however, do not fit such a scheme. Communities of these systems as may be demonstrated by the cushion plant-lichen community are depauperate in both species diversity and biomass and their production is hardly measurable. The turnover rate which can be characterized as energy flow per unit biomass is also extremely low not only because of low production but even more because of slow decomposition. These factors have most probably conditioned the useful protective adaptation: low compact cushion (*Dryas integrifolia, Saxifraga oppositifolia, Silene acaulis*) and the dense compact tuft of sedges (*C. nardina, C. misandra*).

According to Margalef (1963) succession is an exchange of present energy for future biomass. On raised beaches there is so little accumulation of organic matter that any attempt to apply the Margalef's rule means to put the successional process on a geological time scale.

Theoretically every primary succession involves three stages:
a) invasion of pioneer species and their establishment from propagules.
b) stand formation and build up of a "critical" standing crop. Habitat microclimate improvement and increasing competition are finally disadvantageous for most of the primary invaders themselves.
c) some of the original invaders are eliminated and replaced by new invading species, though this is minor in the Arctic (Bliss 1962a).

Raised beaches in association with the adjacent meadows display distinct successional stages along the altitudinal gradient. Some crests represent the first stage, the beginning of the high

arctic primary succession. Only very limited numbers of species can get established here. The only unnecessary preconditioning of the habitat is done by lichens. Plant cover and standing crop increase on slopes but it is the Transition Zone where the community is ready for a change in species composition. New species such as *Carex rupestris*, *C. misandra* and *Cassiope tetragona* enter the community, while *C. nardina* established on crests and slopes is missing completely. Also the proportion of individual species in a community changes, but how much of this is a time successional sequence and how much is a microenvironmental sequence is not easy to say at present.

In a less extreme environment the inexpressive lowland topography would be of no hindrance for the establishment of a substantial vegetation over the entire lowland in a short time. Here, however, this process is very slow. In the last 8000 years only some crests of the oldest beaches have reached the stage of denser plant cover. This indicates the rate of the succession if left to its natural pace.

The question remains whether the process of succession was continuous from time of deglaciation (or emergence of the raised beach from the sea) or whether there were climatic periods in the past which would slow down or stop completely the process.

Small scale climatic changes such as the Hypsithermal period (4000-6000 years BC), Little Climatic Optimum (LCO) in 9-12 century AD and espeically in the Little Ice Age (LIA) 1550-1900 AD (Bray 1971) resulted in marked shifts of major vegetational zones (e.g. tree line) on an altitudinal and latitudinal scale. Undoubtedly these fluctuations in climate, mainly the LIA affected the existing

vegetation in the High Arctic and I believe that also of the raised beaches. Although we do not have much concrete evidence I assume that even slight climatic alteration would result in a dramatic, often "yes or no" response from many vascular species growing in habitats on the fringe of survival. This would apply to Polar Desert Plateaus even more. In the Truelove River valley much thicker remnants of willow stems have been found than occur today on living plants. On the Plateau, larger areas exist with fully developed stands of cushion plants, all of them dead at present. Unfavorable alteration in climate most probably killed them. During LIA not only present ice caps expanded (Ahlman 1953) but very likely some areas were temporarily covered by thin ice crusts which could kill the vegetation and released it undisturbed but dead after they melted. (Bradley 1973).

All this suggests that high arctic ecosystems are youthful and immature not only because of the relative short time from deglaciation (*ca.* 8500 years), lack of soil, etc. (Dunbar 1972, Bliss *et al.*, 1973) but also because of their possible and probable retardation and retrogression during the less favorable climatic anomalies as was the recent Little Ice Age. On the contrary to the subarctic and low-arctic regions where climate alteration caused a real shift in vegetational complexes, in the High Arctic these changes occured merely on the quantitative basis (in terms of standing crop, size of individuals, reproduction potential, etc., within a present type of vegetation). In this threshhod situation, an unfavorable climatic period might bring the retrogression to the very beginning.

Not much is known about the survival potential of high arctic vascular species. Frequency and distribution of important refugia

play an important role. This flora is, however, highly indicative of the microenvironment. Because in vast areas these plants grow far below their optimum requirements it is understandable that their growth might be significantly stimulated if temperature and moisture are artificially increased (as follows from the results of my unpublished "greenhouse" study with the polyethylene sheets laid over the beach ridge community), or if limiting nutrients are directly supplied (see Fig. 40, 41 and Babb and Bliss 1974). In both cases the experimentation resulted in a marked increase in production and plant growth.

The overall ecological significance of raised beaches to the Lowland's ecosystem becomes evident when the Truelove Lowland is compared with some other lowlands and coastal valleys with no raised beach steps but with long and smooth slopes. These lowlands though also protected by cliffs have no real meadows and only very sparse vegetation. The importance of topography as a protecting and supporting factor of the vegetation in the High Arctic is obvious, especially as they retard water movement, as was emphasized by Beschel (1970). Cornwallis Island, has very depauperate vegetation with few real maedows, only where there is local water from melting snow. This results mostly from a limestone substrate which weathers slowly in a water deficient environment. King Christian, Ellef Rignes and to a lesser extent Melville Islands have wide and smooth coastal zones which are predominantly covered by *Luzula-Alopecurus* steppes, poor on species and low in standing crop as well as production (Bliss and Svoboda 1974). On the other hand, Devon Island lowlands (Truelove, Sparbo Hardy, Skogn Lowlands) which are well

protected by cliffs or those which are deeply enclosed in deglaciated fiords and inland valleys (Axel Heiberg, Ellesmere Island) are lush and numerous in species (Lake Hazen area, 82°N and especially Fosheim Peninsula).

With respect to the lowland ecology, raised beaches play an important role in partitioning the lowland area into many smaller units. This results in slowing down water run-off, leaching away of nutrients and creating additional niches for plants and animals, especially lemming.

The high arctic lowlands are analogous to green oases. On the other hand, the vast Polar Deserts of the upland with scattered discontinuous vegetation and almost non-existing higher trophic levels can hardly be classified as fully functional systems. Polar Deserts as vegetational zones represent rather a mosaic of discontinuous microecosystems ranging from small depressions with slightly more concentrated vegetation to single bird perches and isolated plant cushions as was demonstrated with *Dryas integrifolia*. A high permafrost table, poorly developed soils, frequent and gusting winds, sand abrasion and soil erosion, moisture and drought stress are at work most of the time. Moreover at these latitudes, alpine altitudinal conditions decrease to elevations of a few hundred meters above sea level so that most of the upland regions are arctic and alpine at the same time.

Polar Semi-deserts and Deserts represent the cold, dry and nutrient poor margins of terrestrial ecosystems. However, studies at the margins lead to a better understanding of the core of things. Ultimately also this study brought about a fuller look into the

specific as well as general biological and ecological reality, deeper than what follows strictly from results presented in this work. I believe that in this sense Polar Lands and deserts at all have had their substantiation and justification long before science and beyond science. Their very true meaning is in stimulation "to seek answers to questions which cannot be reached in any other way" (Thomas Merton).

SUMMARY

Polar Semi-desert and partially also Polar Desert vascular plant communities were studied on raised beaches of the Truelove Lowland and on the adjacent plateau on Devon Island, N.W.T. for three growing seasons. In the Lowland, raised beaches form an isostatic uplift which has followed the last deglaciation of this area *ca.* 8700 years BP. Raised beaches are similar in shape and structure, relatively well-drained with a maximum depth of active layer *ca.* 100 cm. They contain weakly developed Cryic, Regosolic, Brunisolic and Gleysolic soils. They are low mainly in N, P, organic matter, silt and clay, high in Ca and base saturation. On the Plateau, Polar Desert soils and Lithosols occur with very active frost phenomena. Raised beaches experience higher fluctuations in temperature and moisture than lowland meadows but less than the surrounding plateau.

Three physical and ecological zones, the crest, slope and transition have been recognized on a riased beach, with species diversity, plant cover and standing crop continually decreasing up slope. Crests and slopes are dominated by a "cushion plant-lichen community" with *Dryas integrifolia, Saxifraga oppositifolia, Carex nardina* and *Salix arctica* and 5-7 other infrequent species. The transition zone is occupied by a "cushion plant-moss community" with *D. integrifolia, S. oppositifolia, C. misandra, Cassiope tetragona, S. arctica* and a few additional species. The total vascular plant cover is *ca.* 20% on the crest, 35% on slopes and 58% in transitions. A positive correlation was found between cover, standing crop, and age and elevation of raised beaches. On the plateau vascular plant cover is less than 2% in most areas.

The phenological pattern is correlated with the pattern of snowmelt and starts *ca.* 14 days earlier on the crest than in the transition. *Saxifraga* is the earliest to flower, *Carex* the latest. Differences in flowering intensity exist between crest and transition plants. Some species produce leaves which function more than one season (*D. integrifolia, S. oppositifolia, C. tetragona, C. nardina*). The growth chamber experiment verified that *S. oppositifolia* breaks winter dormancy immediately after snowmelt, at plant temperatures slightly below the freezing point, while *Dryas* needs *ca.* 3°C to show first indications of physiological activity.

On the Intensive Raised Beach Site, total vascular plant standing crop comprises 350 to 400 g . m^{-2} (with the below ground fibric organic matter 700 to 800 g . m^{-2}). Most of the total standing crop is present on slopes, most of the live standing crop is present in the Transition Zone. Standind dead accounts for *ca.* 70% of the aboveground standing crop, green photosynthetic parts of shoots for 3-4% and roots for 15-20%. *Dryas integrifolia* contributes 47% on crests and 77% on slopes to the community standing crop. On the plateau the total vascular standing crop ranges from 0 to 70 g . m^{-2}. Net production of the IRB averaged 21.8 g . m^{-2} in three years with slight variations between years. Seasonal productivity based on a 50 day growing season was 0.43 g . m^{-2} . day^{-1}). On the Plateau net production was *ca.* 2-4.5 g . m^{-2}.

Although a seasonal peak in chlorophyll content exists, no direct correlation between chlorophyll content and production was observed. Community leaf area index was only *ca.*0.1. Carbohydrate values were very low in woody *Dryas* and semi-woody *S. oppositifolia*

(1-2%), increased to 6-7% in *C. nardina* and reached 30% in roots of soft herbs such as *Pedicularis lanata*. Most of the soluble sugars are stored in a form of oligosaccharides. Lipids in crest plants were higher (3-6%) than in plants growing in the transition zone (2.5-5.5%). Ash free caloric values were 5259 in *D. integrifolia*, 4840 in *S. oppositifolia* and 4731 cal . g^{-1} in *C. nardina*. The highest value was obtained from roots of *S. oppositifolia* (6000 cal . g^{-1}). Special attention was devoted to the ecology of *D. integrifolia*. In the cushion, six different strata of old leaves were analyzed for carbohydrate, ash, and caloric content in order to estimate their decomposition rates, and on the cushion surface, leaf angle orientation was measured. The *Dryas* cushion was found to be well adapted to resist extremes in the microclimate, to recover nutrients released by decomposition of its own decaying parts, and therefore, the cushion can be considered as an efficient, semi-closed, microecosystem.

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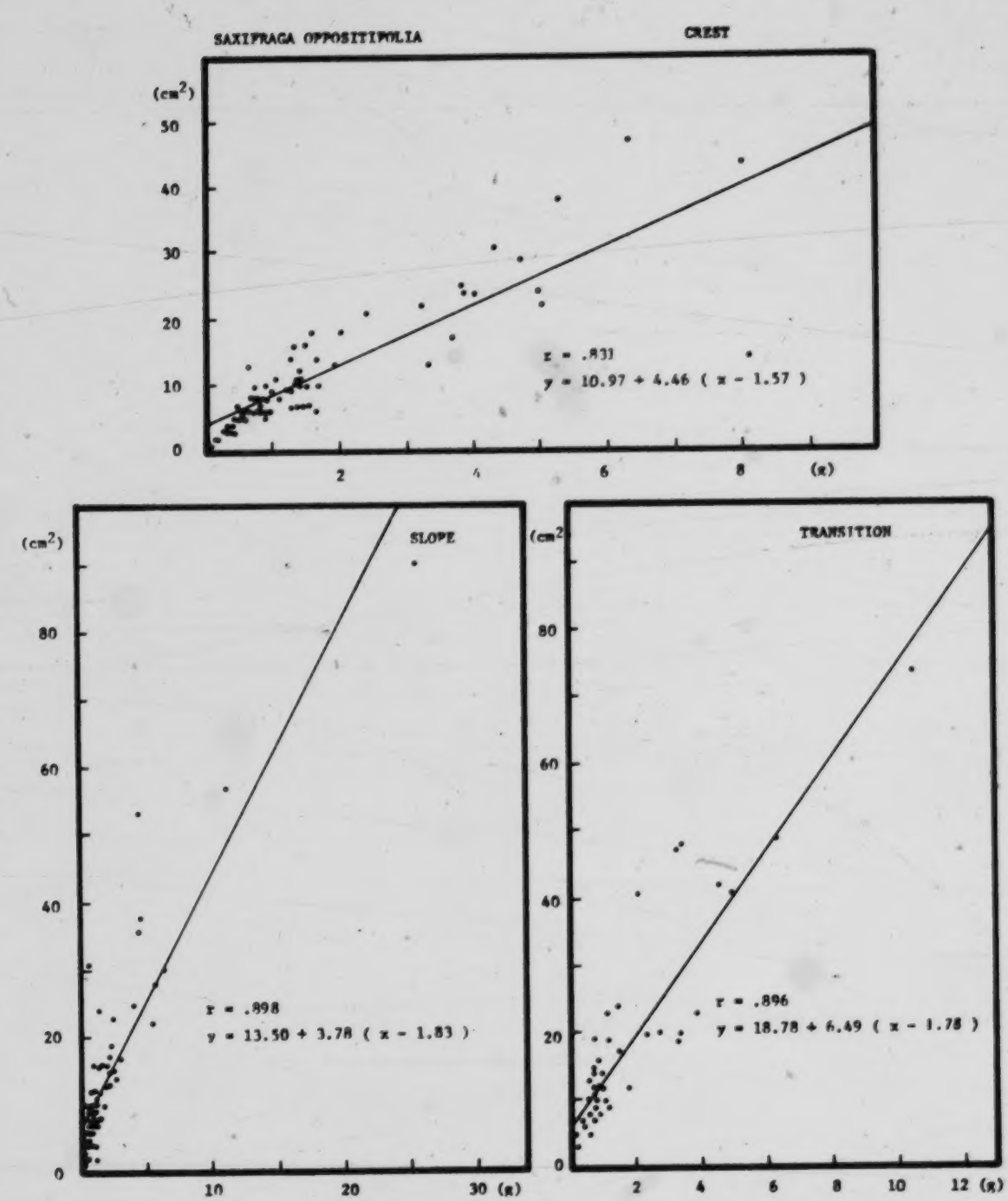
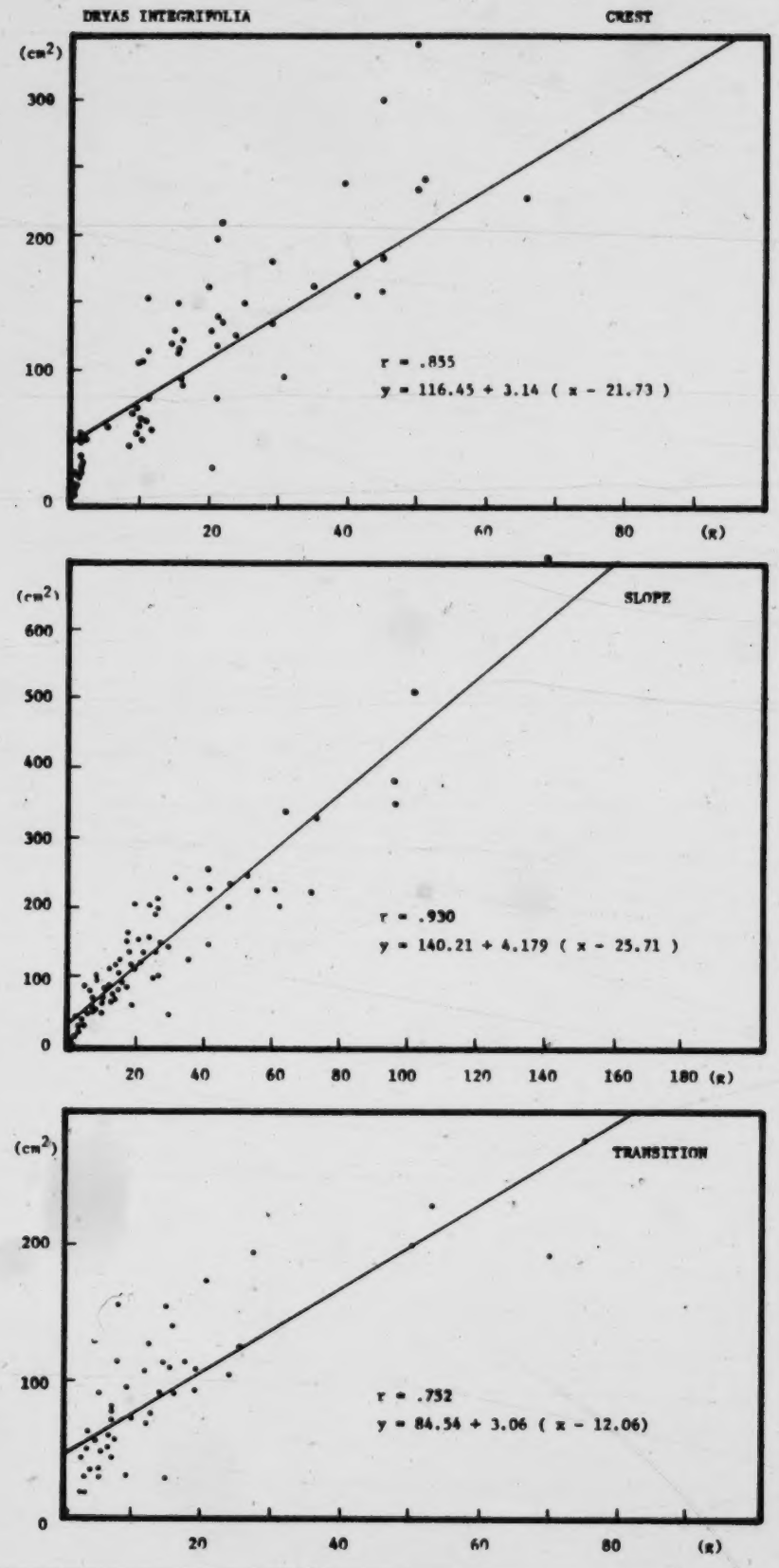


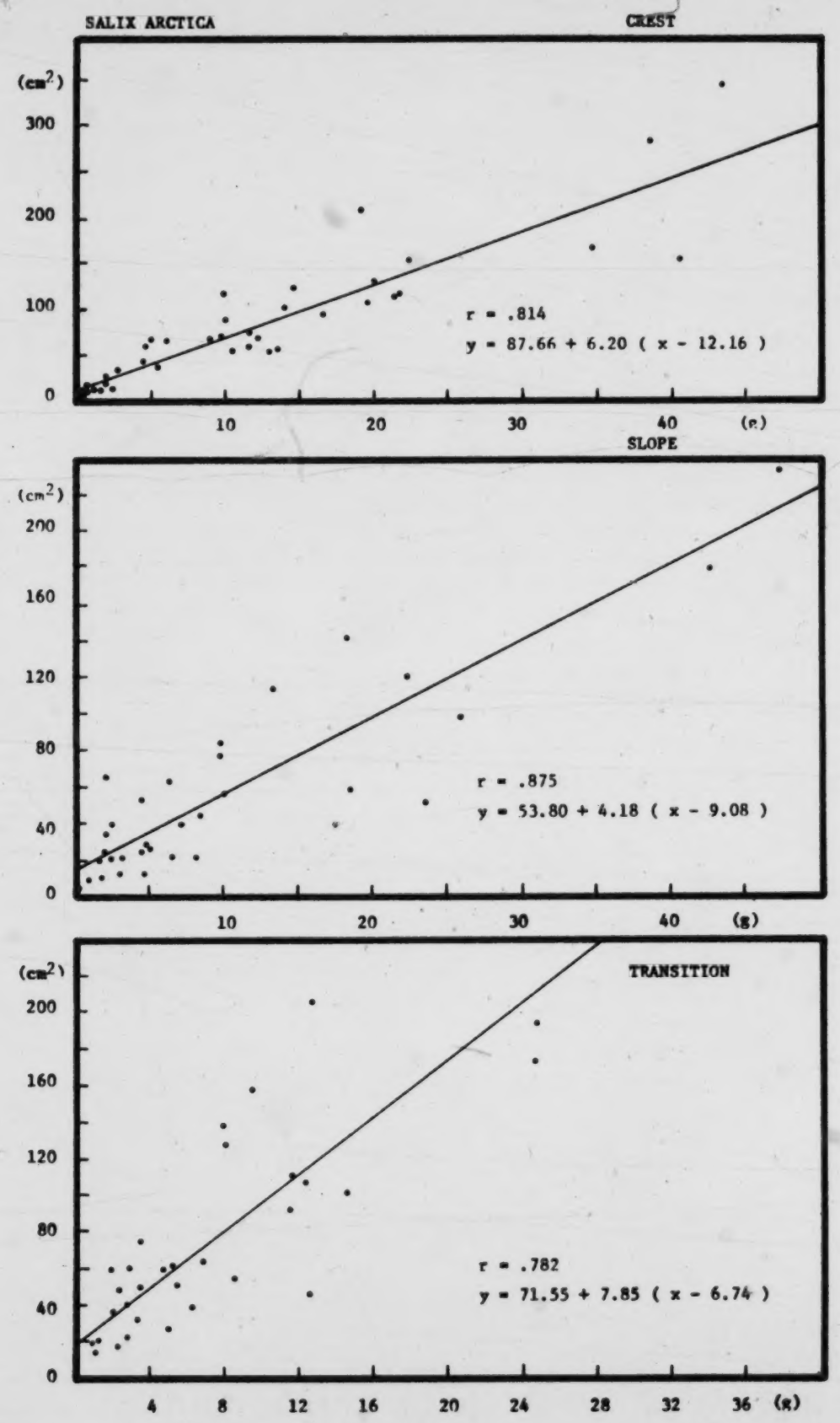
Appendix 1a

Ground area of an individual plant (cm^2) versus its total standing crop (g) in three zones of the Intensive Raised Beach. 1971.



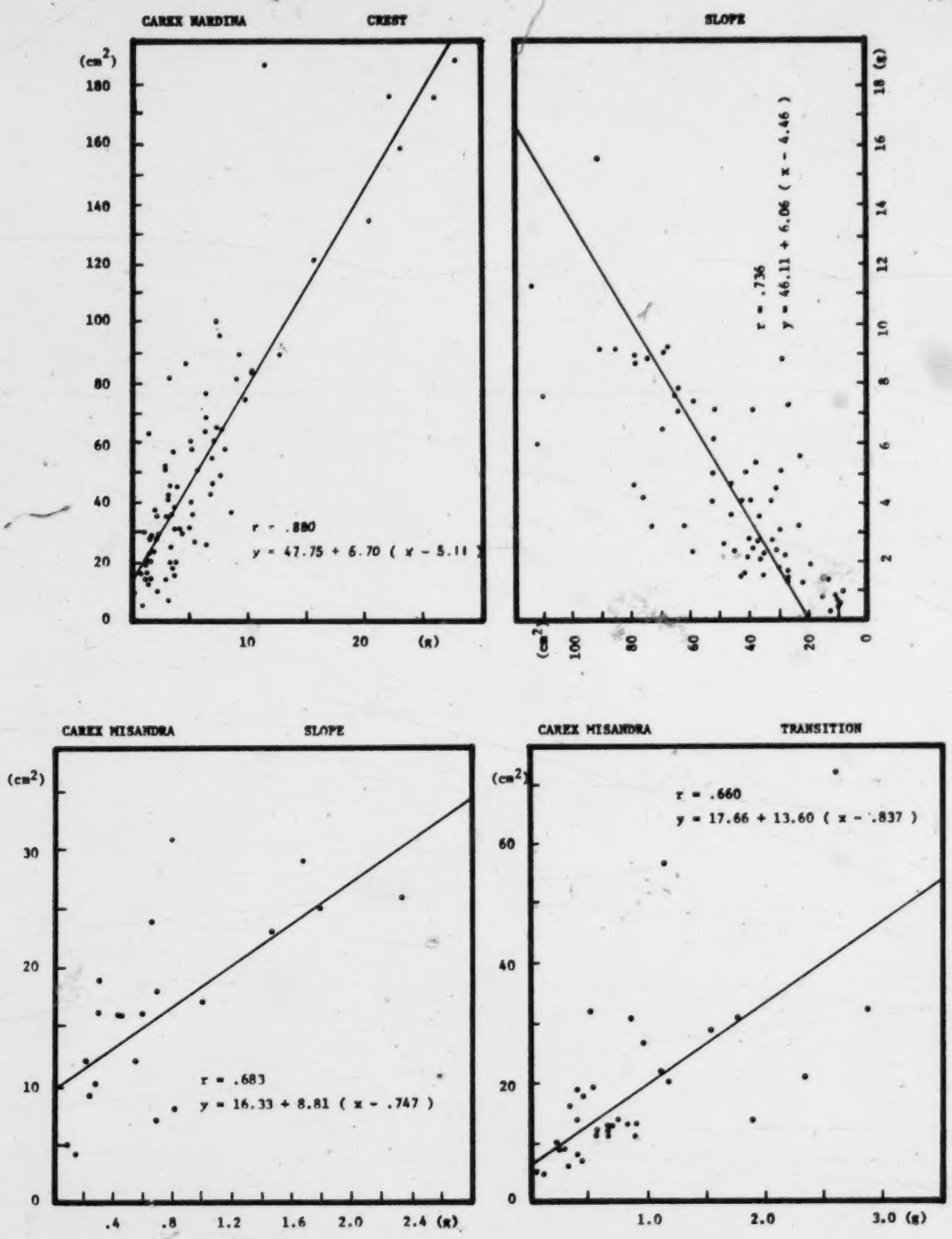
Appendix 1b

Ground area of an individual plant (cm^2) versus its total standing crop (g) in three zones of the Intensive Raised Beach. 1971.



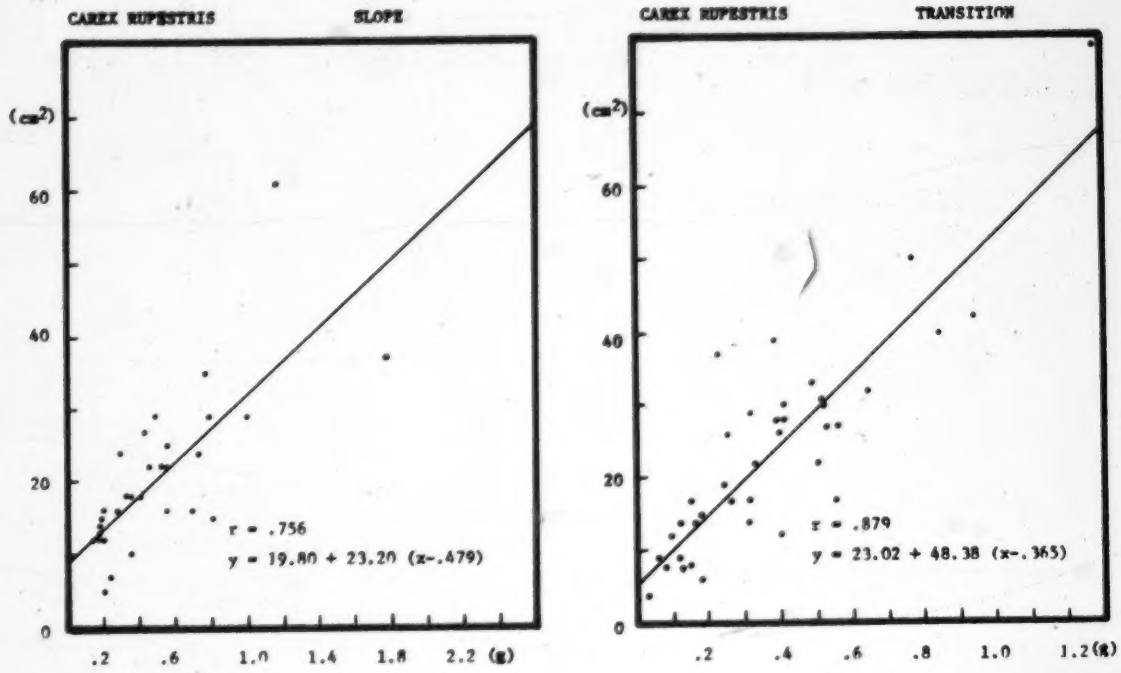
Appendix 1c

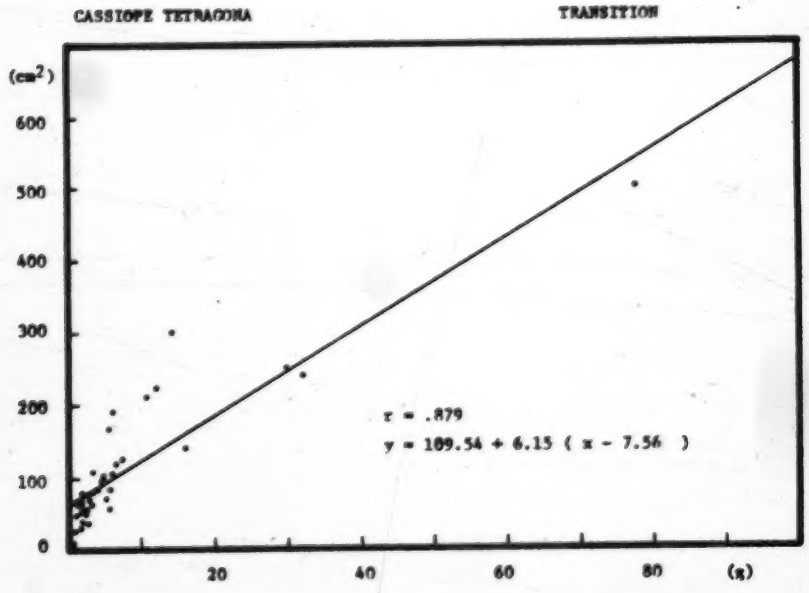
Ground area of an individual plant (cm^2) versus its total standing crop (g) in three zones of the Intensive Raised Beach. 1971.



Appendix 1d

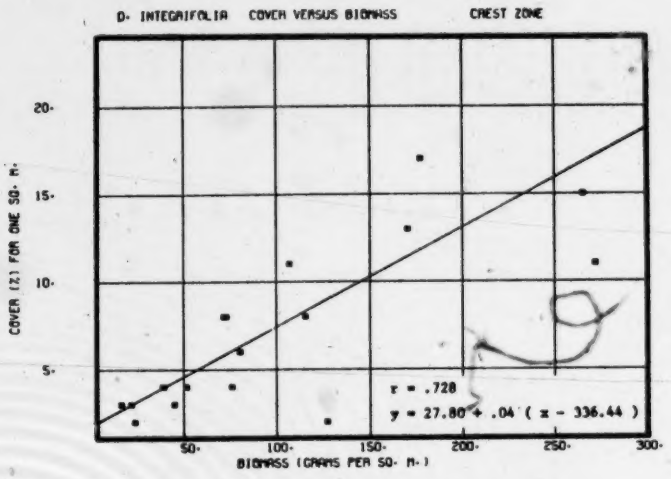
Ground area of an individual plant (cm^2) versus its total standing crop (g) in three zones of the Intensive Raised Beach. 1971.

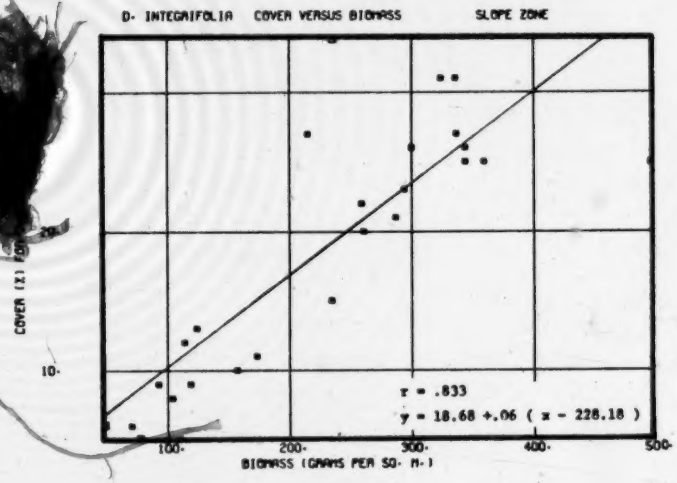


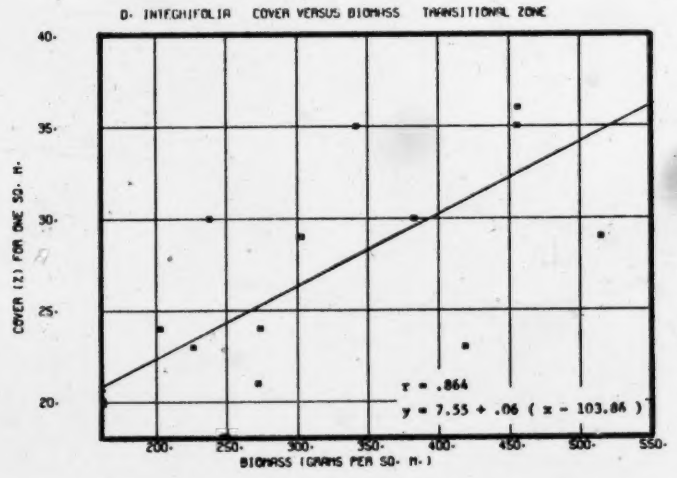


Appendix 1e

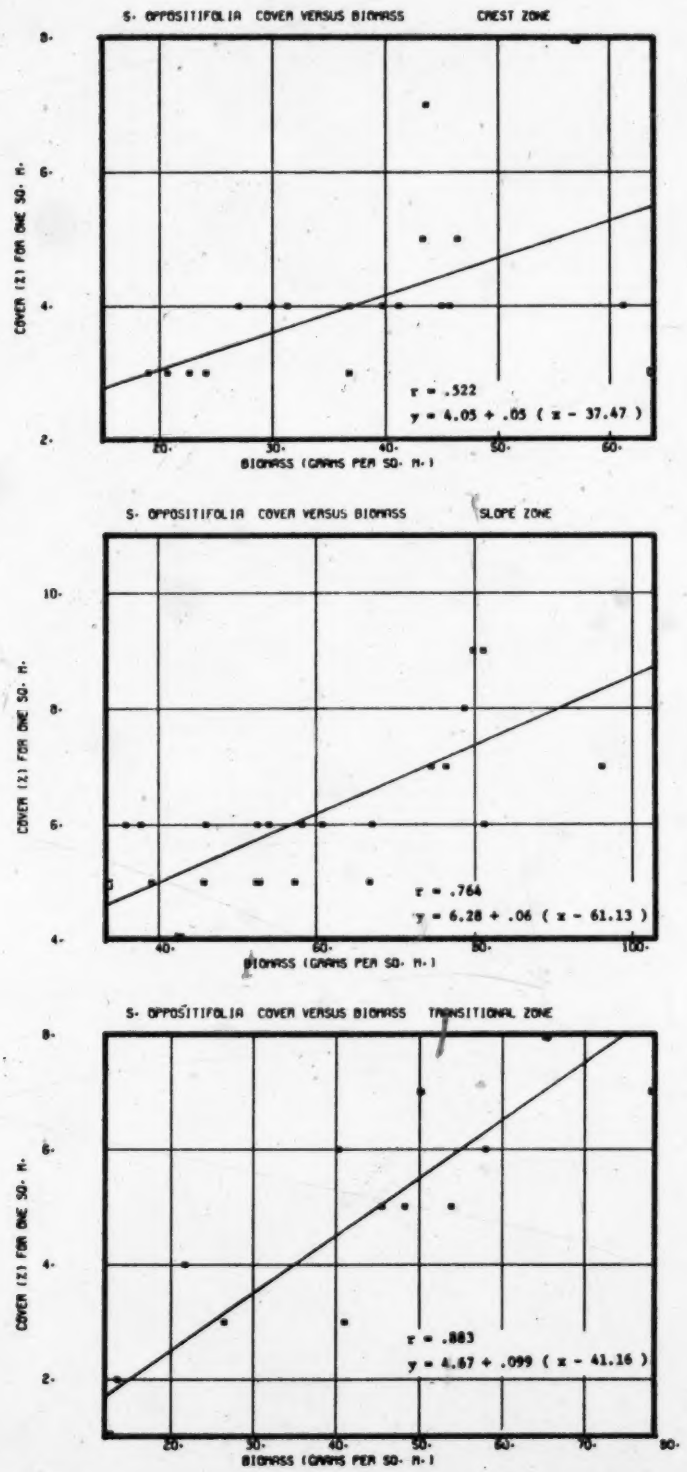
Ground area of an individual plant (cm^2) versus its total standing crop (g) in three zones of the Intensive Raised Beach. 1971.



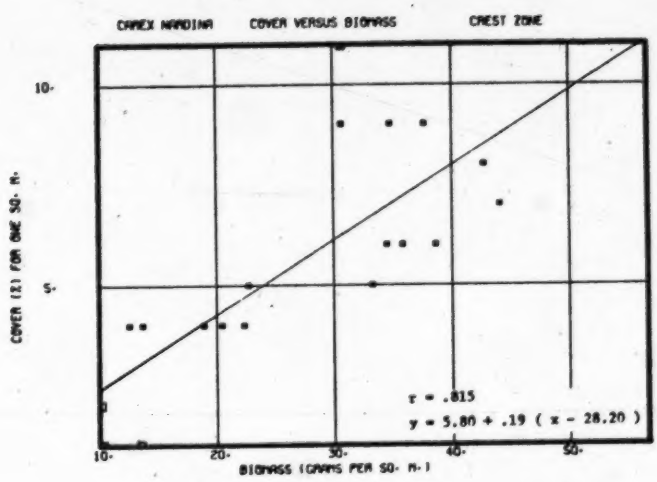


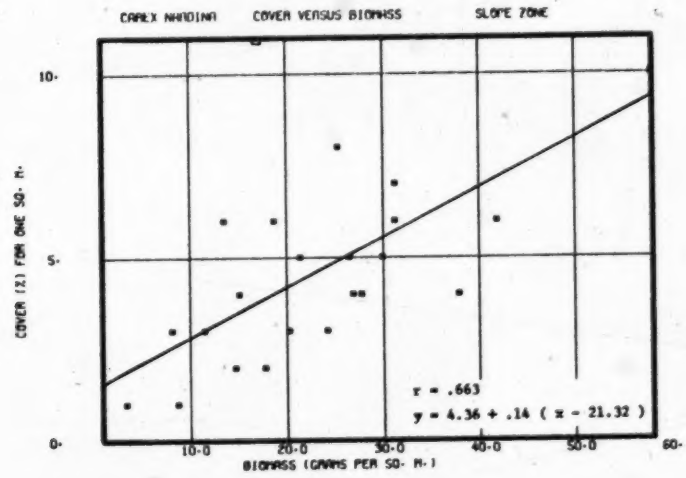


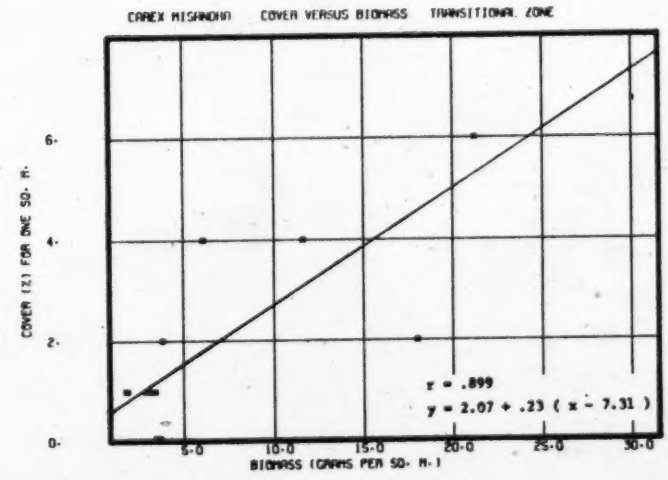
Appendix 2a Cover (%) of individual species versus the total standing crop (g m^{-2}) of this species in three zones of intensive Beach Ridge 1971.


S. OPPOSITIFOLIA COVER VERSUS BIOMASS CREST ZONE
COVER (%) FOR ONE SQ. M.
BIOMASS (GRAMS PER SQ. M.)
r = .522
y = 4.05 + .05 (x - 37.47)
S. OPPOSITIFOLIA COVER VERSUS BIOMASS SLOPE ZONE
COVER (%) FOR ONE SQ. M.
BIOMASS (GRAMS PER SQ. M.)
r = .764
y = 6.28 + .06 (x - 61.13)
S. OPPOSITIFOLIA COVER VERSUS BIOMASS TRANSITIONAL ZONE
COVER (%) FOR ONE SQ. M.
BIOMASS (GRAMS PER SQ. M.)
r = .883
y = 4.87 + .099 (x - 41.16)

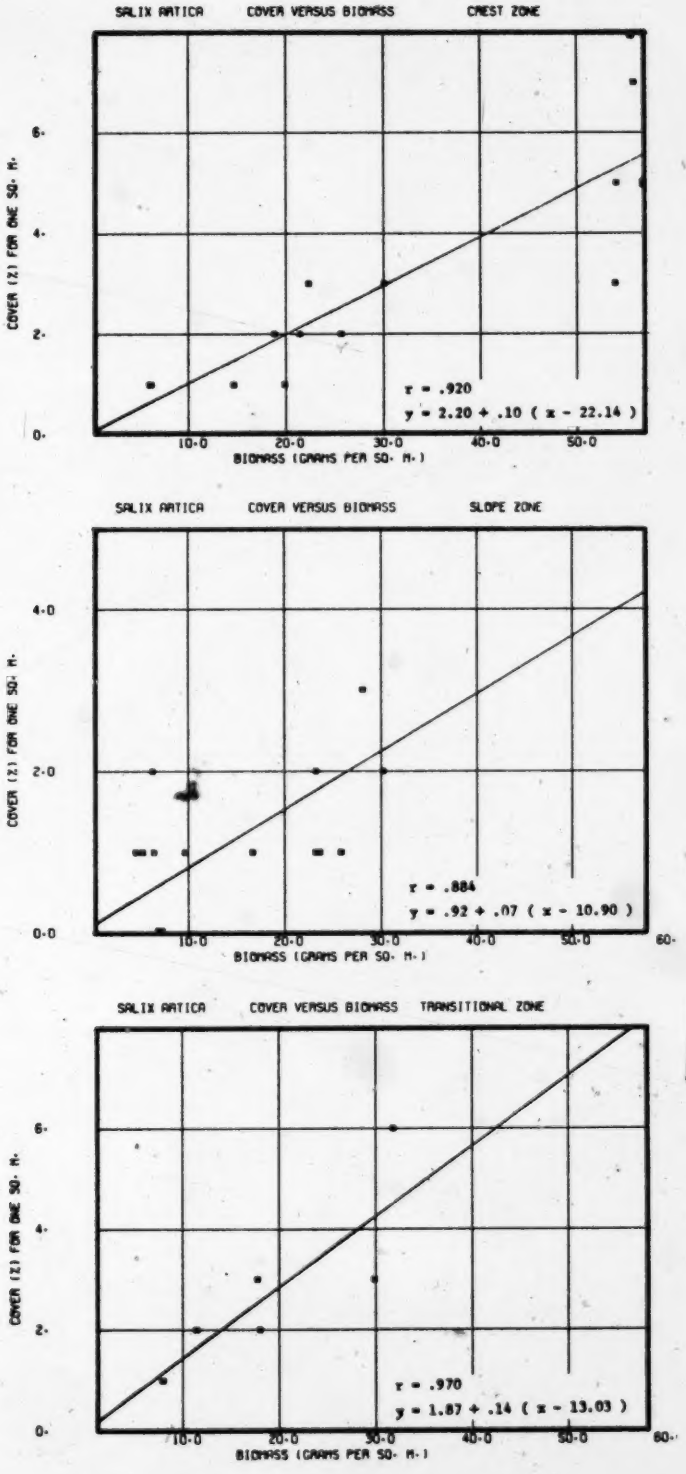
Appendix 2b Cover (%) of individual species versus the total standing crop (g m^{-2}) of this species in three zones of Intensive Beach Ridge 1971.



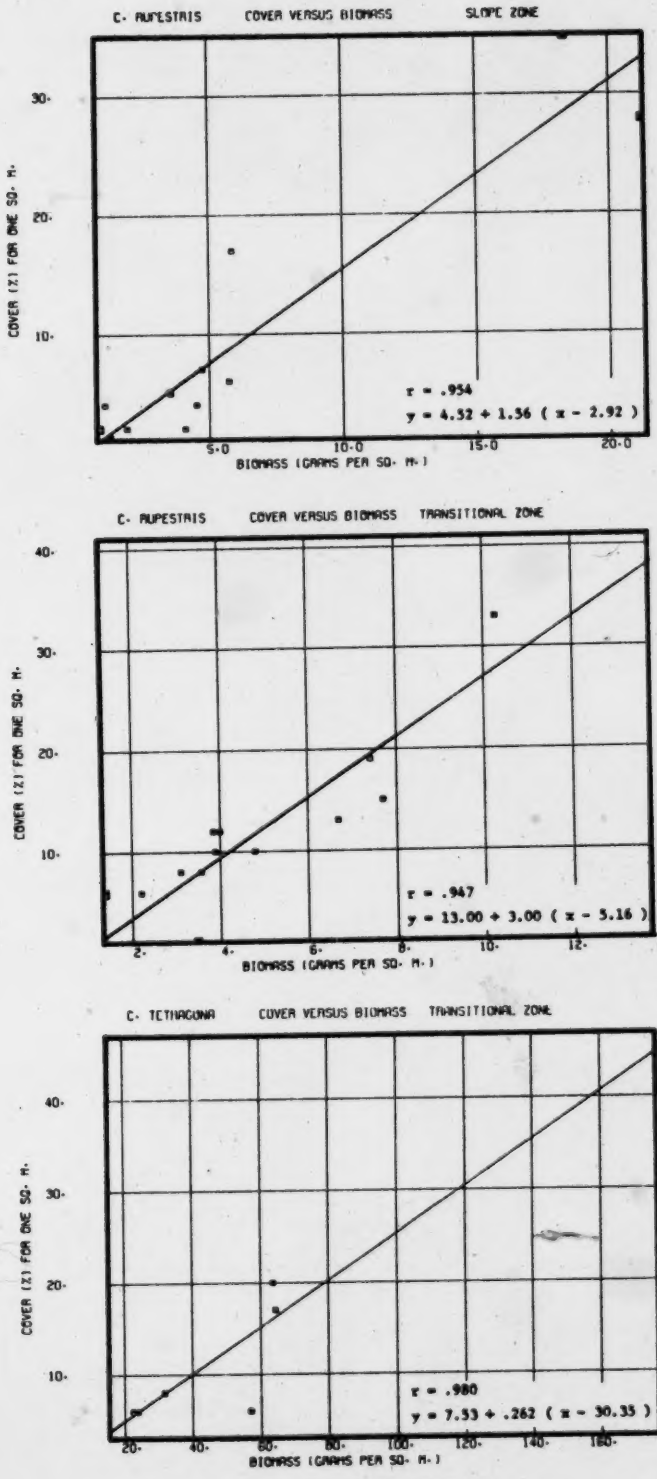




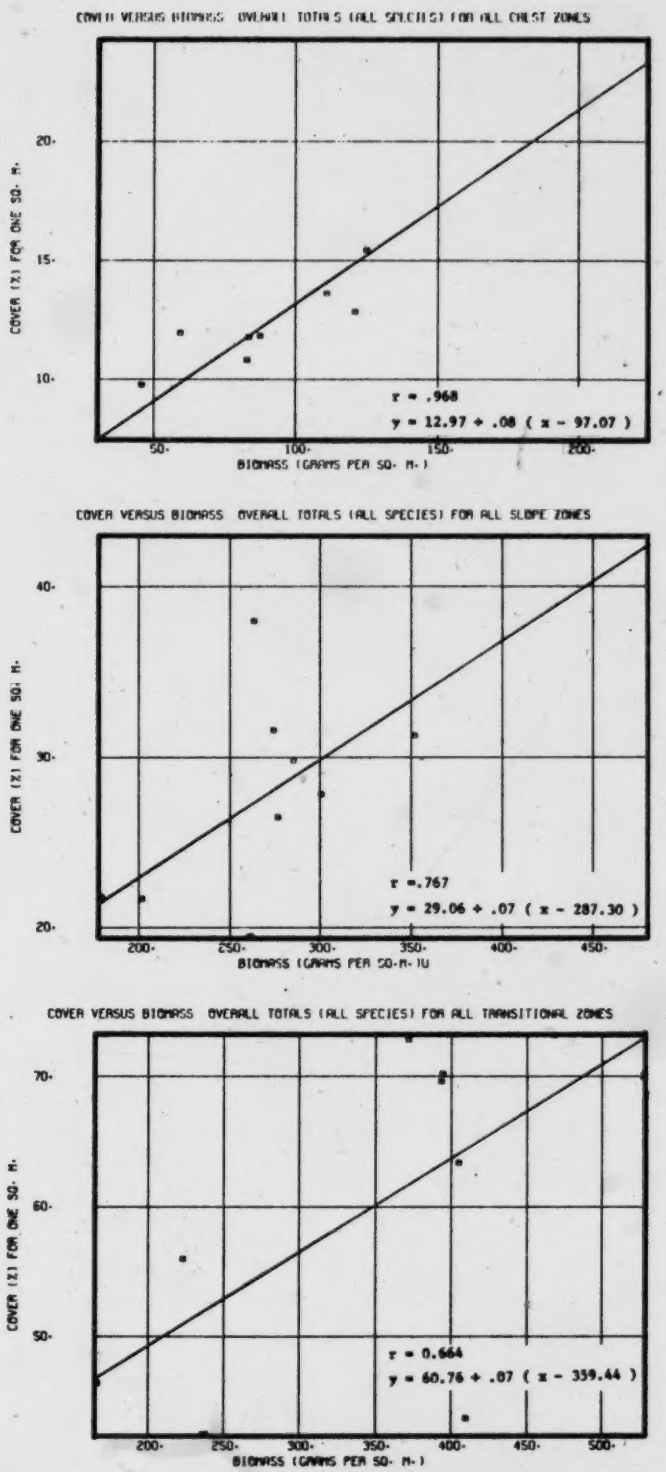
Appendix 2C Cover (%) of individual species versus the total standing crop (g m^{-2}) of this species in three zones of intensive Beach Ridge 1971.


SALIX ARTICA COVER VERSUS BIOMASS CREST ZONE
COVER (%) FOR ONE SQ. M.
BIOMASS (GRAMS PER SQ. M.)
r = .920
y = 2.20 + .10 (x - 22.14)
SALIX ARTICA COVER VERSUS BIOMASS SLOPE ZONE
COVER (%) FOR ONE SQ. M.
BIOMASS (GRAMS PER SQ. M.)
r = .884
y = .92 + .07 (x - 10.90)
SALIX ARTICA COVER VERSUS BIOMASS TRANSITIONAL ZONE
COVER (%) FOR ONE SQ. M.
BIOMASS (GRAMS PER SQ. M.)
r = .970
y = 1.87 + .14 (x - 13.03)

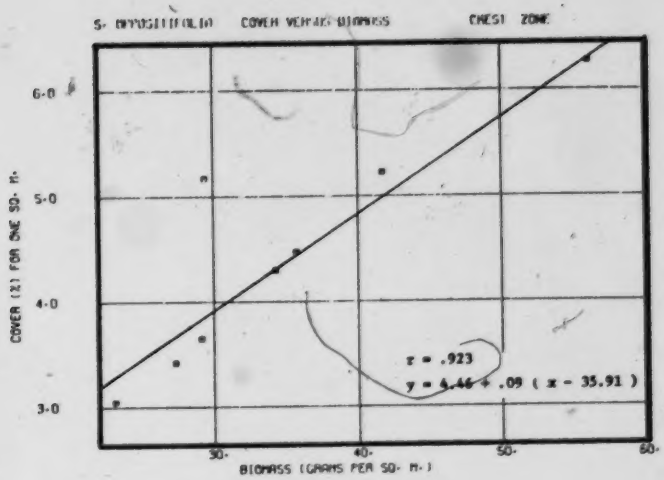
Appendix 2d Cover (%) of individual species versus the total standing crop (g m^{-2}) of this species in three zones of intensive Beach Ridge 1971.

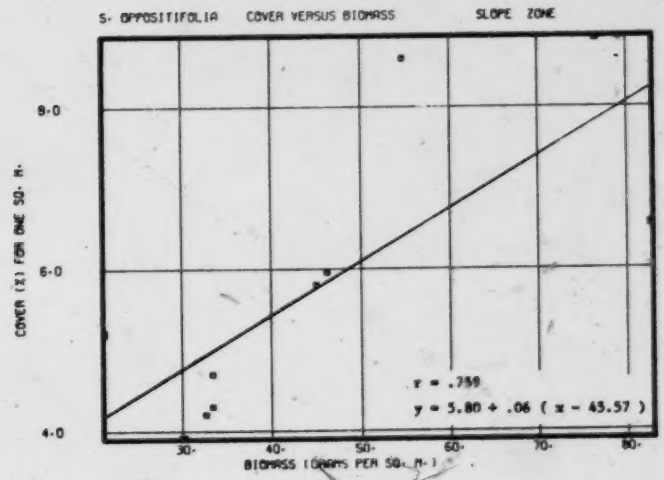

C. RUPESTRIS COVER VERSUS BIOMASS SLOPE ZONE
COVER (%) FOR ONE SQ. M.
BIOMASS (GRAMS PER SQ. M.)
r = .954
y = 4.32 + 1.56 (x - 2.92)
C. RUPESTRIS COVER VERSUS BIOMASS TRANSITIONAL ZONE
COVER (%) FOR ONE SQ. M.
BIOMASS (GRAMS PER SQ. M.)
r = .947
y = 13.00 + 3.00 (x - 5.16)
C. TETRAGONA COVER VERSUS BIOMASS TRANSITIONAL ZONE
COVER (%) FOR ONE SQ. M.
BIOMASS (GRAMS PER SQ. M.)
r = .980
y = 7.53 + .262 (x - 30.35)

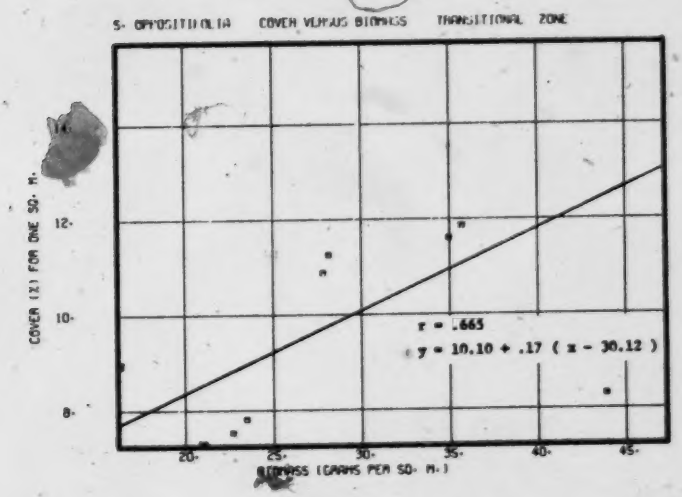
Appendix 2c Cover (%) of individual species versus the total standing crop (g m^{-2}) of this species in three zones of intensive Beach Ridge 1971.


COVER VERSUS BIOMASS OVERALL TOTALS (ALL SPECIES) FOR ALL CREST ZONES
COVER (%) FOR ONE SQ. M.
BIOMASS (GRAMS PER SQ. M.)
r = .968
y = 12.97 + .08 (x - 97.07)
COVER VERSUS BIOMASS OVERALL TOTALS (ALL SPECIES) FOR ALL SLOPE ZONES
COVER (%) FOR ONE SQ. M.
BIOMASS (GRAMS PER SQ.M.)
r =.767
y = 29.06 + .07 (x - 287.30)
COVER VERSUS BIOMASS OVERALL TOTALS (ALL SPECIES) FOR ALL TRANSITIONAL ZONES
COVER (%) FOR ONE SQ. M.
BIOMASS (GRAMS PER SQ. M.)
r = 0.664
y = 60.76 + .07 (x - 339.44)

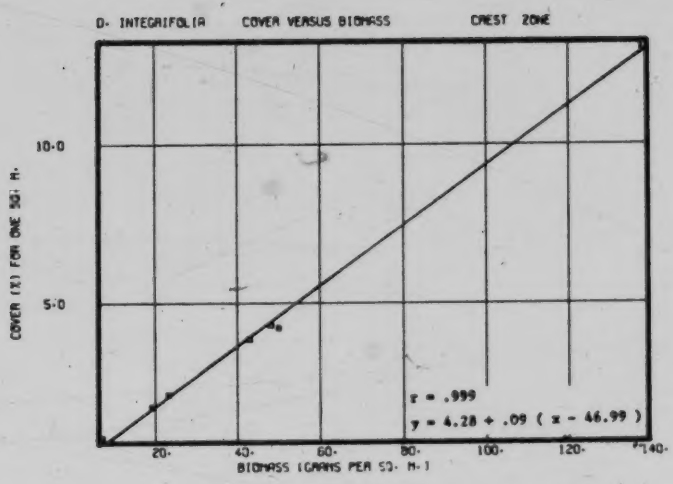
Appendix 3 Community cover (%) versus the aboveground standing crop (g m^{-2}) in 10 Truelove Lowland raised beaches. Extensive sampling program 1971.

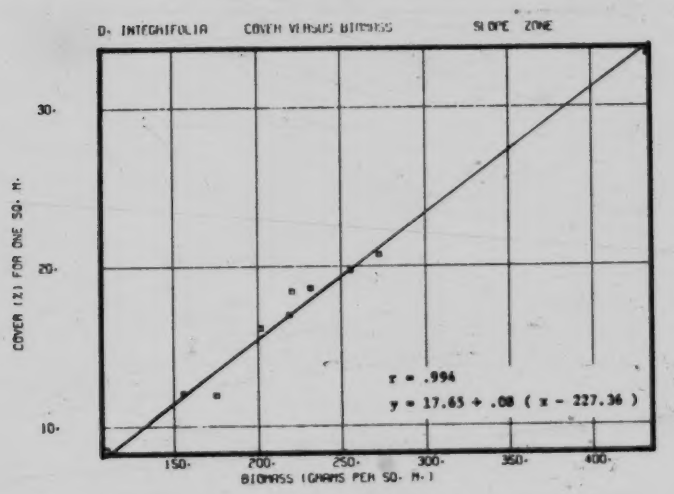


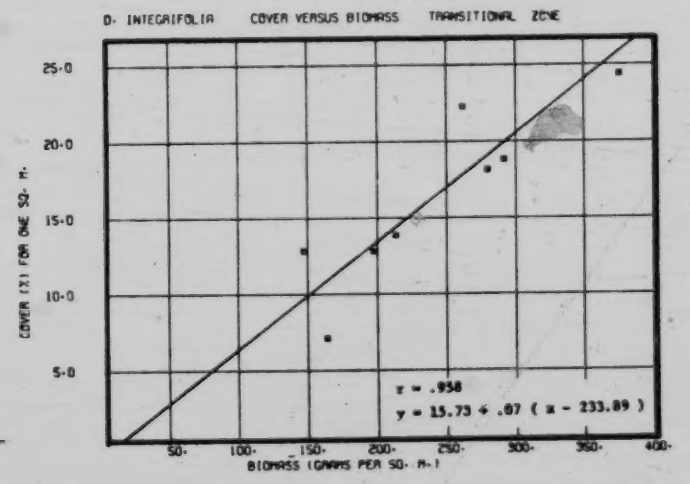




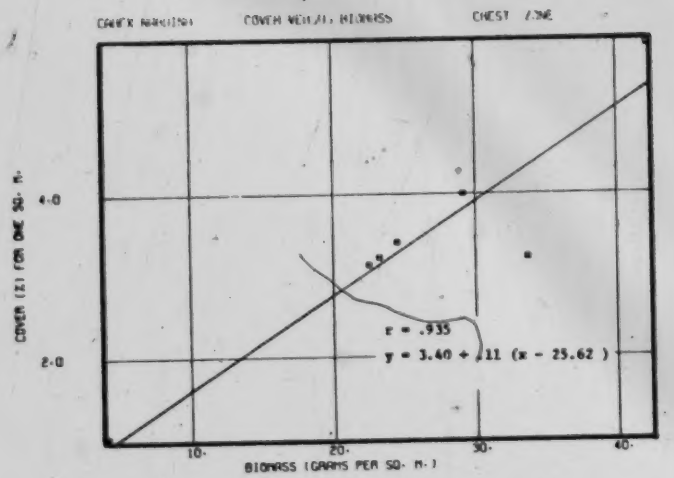
Appendix 4g Cover (%) of individual species versus the aboveground standing crop (g m^{-2}) of this species in 10 Truelove Lowland raised beaches. Extensive sampling program 1972.

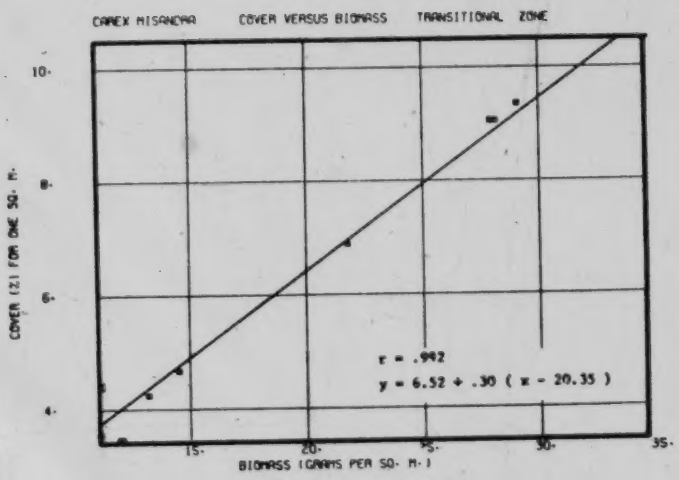


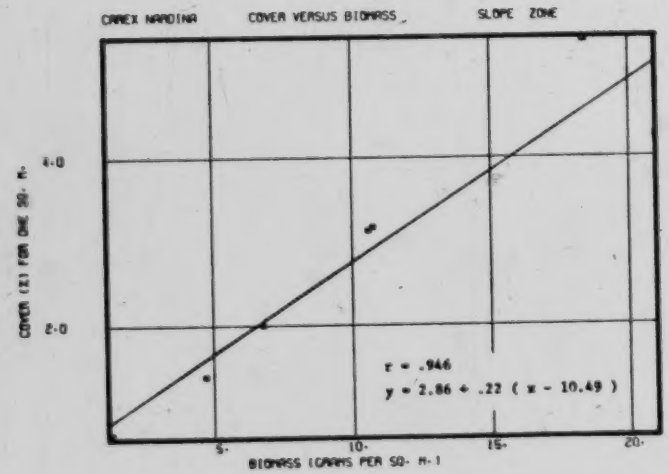


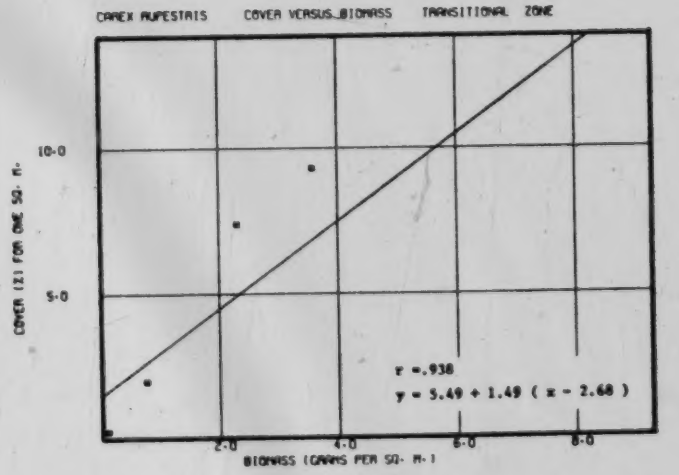


Appendix 4b Cover (%) of individual species versus the aboveground standing crop (g m^{-2}) of this species in 10 Treelove Lowland raised beaches. Extensive sampling program 1972.

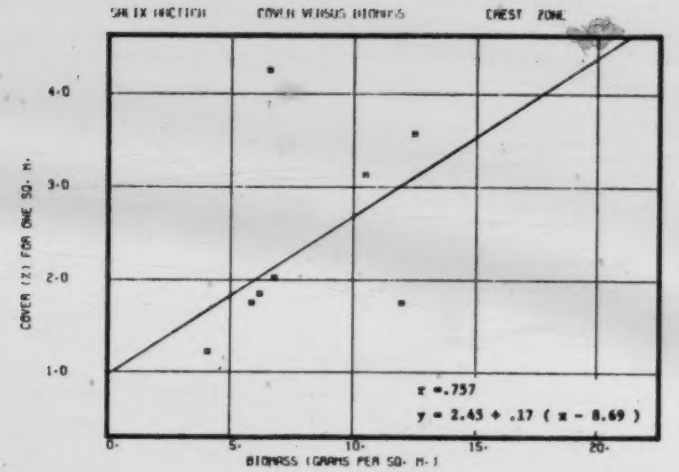


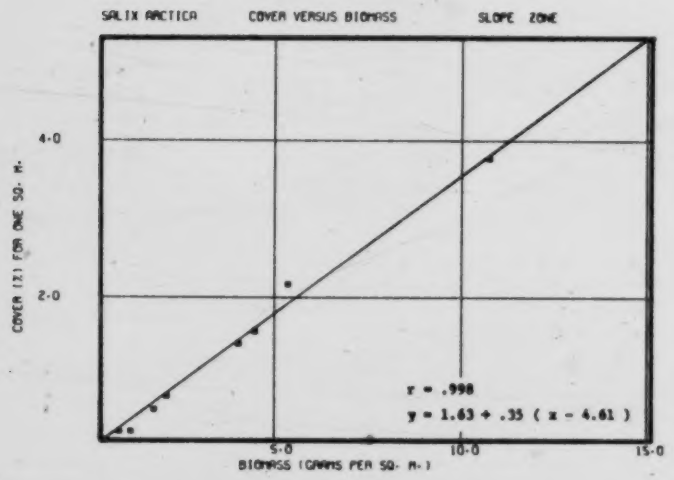


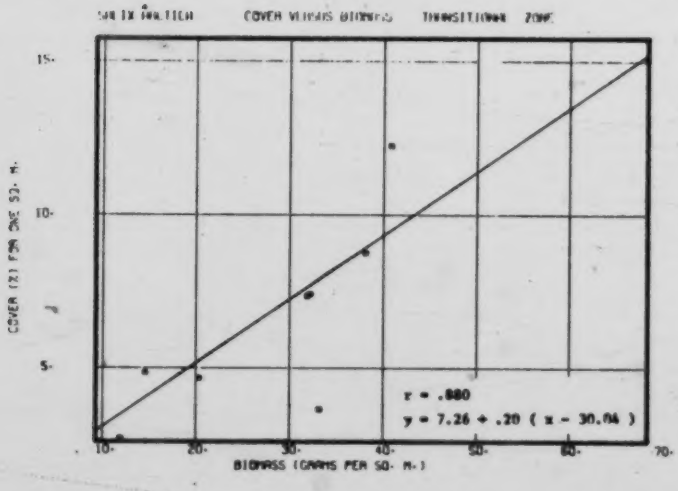




Appendix 4c Cover (%) of individual species versus the aboveground standing crop (g m^{-2}) of this species in 10 Truelove Lowland raised beaches. Extensive sampling program 1972.







Appendix 4d Cover (%) of individual species versus the aboveground standing crop (g m^{-2}) of this species in 10 Truelove Lowland raised beaches. Extensive sampling program 1972.